Genetic Variation in Britain

Edited by
D. F. Roberts
and
E. Sunderland

GENETIC VARIATION IN BRITAIN

SOCIETY FOR THE STUDY OF HUMAN BIOLOGY

Although there are many scientific societies for the furtherance of the biological study of man as an individual, there has been no organization in Great Britain catering for those (such as physical anthropologists or human geneticists) concerned with the biology of human populations. The need for such an association was made clear at a Symposium at the Ciba Foundation in November 1957, on "The Scope of Physical Anthropology and Human Population Biology and their Place in Academic Studies". As a result the Society for the Study of Human Biology was founded on May 7th, 1958, at a meeting at the British Museum (Natural History).

The aims of the Society are to advance the study of the biology of human populations and of man as a species, in all its branches, particularly human variability, human genetics and evolution, human adaptability and ecology.

At present the Society holds two full-day meetings per year—a Symposium (usually in the autumn) on a particular theme with invited speakers, and a scientific meeting for proffered papers. The papers given at the Symposia are published and the monographs are available to members at reduced prices.

Persons are eligible for membership who work or who have worked in the field of human biology as defined in the aims of the Society. They must be proposed and seconded by members of the Society. The subscription is £3 per annum (this includes the Society's journal *Annals of Human Biology*) and there is no entrance fee.

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PUBLICATIONS OF THE SOCIETY

Symposia, Volume I, 1958: *The Scope of Physical Anthropology and Its Place in Academic Studies*, edited by D. F. Roberts and J. S. Weiner (out of print).

Symposia, Volume II, 1959: *Natural Selection in Human Populations*, edited by D. F. Roberts and G. A. Harrison. Pergamon Press (members £1).

Symposia, Volume III, 1960: *Human Growth*, edited by J. M. Tanner. Pergamon Press (members 53p).

Symposia, Volume IV, 1961: *Genetical Variation in Human Populations*, edited by G. A. Harrison. Pergamon Press (members £1).

Symposia, Volume V, 1963: *Dental Anthropology*, edited by D. R. Brothwell. Pergamon Press (members £1.25).

Symposia, Volume VI, 1964: *Teaching and Research in Human Biology*, edited by G. A. Harrison. Pergamon Press (members £1.25).

Symposia, Volume VII, 1965: *Human Body Composition, Approaches and Applications*, edited by J. Brozek. Pergamon Press (members £3).

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Symposia. Volume X, 1971: *Biological Aspects of Demography*, edited by W. Brass. Taylor & Francis (members £1.90).

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GENETIC VARIATION IN BRITAIN

Edited by
D. F. ROBERTS and E. SUNDERLAND

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PREFACE

THE continuing growth of interest in human biology in Britain, the steady development of the Society and the expansion of its activities, led the Committee to consider the desirability of extending its Annual Symposium, so that it covered more than a single day. The theme for 1972 "Genetic variation in Britain" represents a long-standing interest of both of us, and we felt that there might perhaps be sufficient research activity to provide material for such an extended discussion. When we set about drawing up the programme, we were surprised to find how much work was indeed in progress—it would have been possible to redouble the length of the meeting. We were therefore selective, omitting though regretfully all mention of the interesting studies of clinical genetic variation, the clines and local specificities that are here emerging; the painstaking work that is in progress in chromosomal variation in different sections of the population; variation of normal gene frequencies with disease; and many others. Instead we concentrated on three topics. First genetic demography, studying variation in the demographic determinants of genetic structure of populations; secondly the distribution of single-gene normal variants, seeking to demonstrate the extent of local and regional differences in gene frequency; and thirdly variation in polygenic characters, with particular emphasis on skin colour and dermatoglyphics.

The papers presented at that meeting are reproduced here, together with several other articles, invited for comparison or to fill gaps in these topics that were not otherwise covered. We are grateful to Professor Walter, Dr. Masterson, Dr. Lincoln, Dr. Dodd and Dr. Welch for sending us manuscripts for this purpose.

The meeting was held in the Zoology Department, Oxford, on April 13th–14th, 1972, participants being accommodated in Hertford College, Oxford. To the Department and to the College for their hospitality, and to Dr. Hiorns who undertook all the local arrangements and made the meeting the success it was, grateful thanks are expressed.

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THE ORIGINS OF GENETIC VARIATION IN BRITAIN

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> "The ever increasing rapidity of local migration and intermixture, due to the extension of railways and the altered conditions of society, will in the next generation almost inextricably confuse the limits and proportions of the British races."

So wrote Beddoe in 1885, and it may appear that the subject of this 1972 Symposium is a century too late. If only Beddoe had had the armamentarium of techniques that is now available for analysis of genetic characters! Certainly people in different parts of Britain today have more interests in common than a century ago. They see the same television programmes, read the same great newspapers, buy the same products in shops of the same name, follow the fortunes of the same football teams. Yet regional interests and traditions persist. One cannot help noticing that the place names differ, that the local dialect contains characteristic words, that speech carries its own local lilt. Some cultural differences then still remain. It is therefore possible that any genetic variation that accompanied the establishment of local cultures also persists. Certainly today individuals and families move according to whim or the requirements of occupation, and gene-flow between regions thereby continues at a rate greater than in historical times, but most traceable forebears of most people, especially in the provinces and rural areas, are found to have lived in the same region as their present day descendants. Hence to seek genetic variation is not profitless. If it exists, then it is important to record it now while there is yet time. For just as Beddoe noted the increased mobility and resulting mixture that the coming of the railways would bring, so the mobility of the late twentieth century that far outweighs anything that he could conceive will cause any remaining genetic heterogeneity indeed rapidly to disappear.

The interest is more than academic. The publication of the national atlas of disease mortality (1963) in the United Kingdom focused attention sharply on the geographical patterns that exist in mortality from specific causes. Some are indeed striking, for example the concentration of mortality from cancer of the stomach, particularly in north Wales, but also in the northern counties of England. For morbidity there is the striking gradient in central neural tube malformations (Carter 1969) which increase steadily in frequency as one moves north and west across Britain, and many others. Explanations of these geographical patterns have been sought in terms of some environmental variable, e.g. the geology, the degree of hardness of the water. Yet differences in the genepools of the regional populations, with differing frequencies of the genes responsible for susceptibility to the development of these disorders, is at least as likely an explanation. Demonstration of similar variation in frequencies of some other genes, particularly those governing normal variant characters, is the first step in establishing such a hypothesis.

The Coming of the Genes

Evidence for the origin of genetic variation in Britain though indirect is strong. Contributions come from several sources—early documentation, history and tradition, archaeology, linguistics, personal and place names. The least evidence is biological, and genetic evidence almost non existent. Analysis of the indirect sources would occupy volumes, but a brief summary of history through genetical eyes, though incomplete, may be helpful in understanding the implications of what follows. All sources testify to the successive invasions and immigrations on varying scales into these islands, for right from the earliest times Britain's position in relation to Europe meant that she received stream after stream of settlers from different parts of the continent, and these have given rise to the varying physical features of the inhabitants recorded by so many authors. T. H. Huxley (1890) pointed out that the duality of the population in southern Britain in Roman times was "one of the few fixed points in British ethnology", Strabo noted that the prisoners taken in southeast Britain were 6 inches taller than the tallest men in Rome and were blonde, whereas by contrast in the interior of the country, Caesar says, dwelt a different people who regarded themselves as autochthonous. The swarthy complexion and curled hair of the Silures of south Wales suggested to Tacitus derivation from Spain, while the reddish hair and large limbs of the Caledonians indicated German affinities. On the peopling of Britain, and the retention of population differences, the geography of the country had very considerable influence. The main physical features of the British Isles profoundly affected the routeways of immigrants, the nature of the landscape their decision on where to settle, and geographical details their subsequent movements.

Small bands of palaeolithic men wandered across Britain, hunted and drifted in the long intervals of ice recession during the Pleistocene, living in small family bands. After the final retreat of the ice, as game and vegetation increased with the warming of climate, the population increased to thousands instead of dozens, and the Mesolithic culture period developed. It is possible that there may be genes from these earliest inhabitants still in the genepool in parts of Britain. But the waves of the neolithic revolution were soon to lap against the shores of Britain, the greater security of food production allowing further population increase, and with the stimulation of more numerous individual contacts came quicker development of new techniques. A powerful megalithic civilization spread over the whole of Ireland and the highland zone of Britain, the culture having been brought by sea from the south and west, that is from Spain and Atlantic France, while into the east of Britain from across the North Sea came the Beaker folk. These newcomers must have brought their genes with them as well as their culture, so that population differences may well have coincided as early as this with the two cultural provinces whose existence was demonstrated by the distribution studies of Chitty and Fox (1932) and which persisted throughout early history. Clues to discrete population distributions are illustrated in Figs. 1 and 2. Invasion of southeast and east Britain from the French, Flemish and German coasts tended to spread generally over the lowland zone. Invasion was frequent, groups of men and materials could cross the narrow seas quickly, cultures succeeded each other in rapid succession, each invasion tending to destroy the influences of its predecessor—a zone of cultural replacement and probably much genepool fluidity. By contrast the western region received its new contacts in smaller doses, perhaps by trading and occasional raiding rather than by massed invasion, so that already-existing cultures tended to absorb the new infiltrations, old customs and old ideas lived long, giving continuity of tradition, and probably also continuity and slow infiltration of genepools.

By the late Bronze age, the culture had spread over the whole of Britain. It is unlikely that this meant the elimination of the earlier population from the north and west, but rather the gradual diffusion of new improved ideas from one group to its neighbours. The Bronze age population avoided the lowest lands and the heaviest soils as too wet or too wooded for occupation, avoided the highest as too exposed, but settled freely in the upland valleys and on shelves of land in the foothills between the mountains and the valley bottoms. Settlement was particularly dense in eastern Northumberland, with penetration up the Tweed and through the Tyne gap into the Eden basin; the dales of the central Pennines, especially Airedale, carrying a similar penetration over the watershed into the Ribble valley; the Derbyshire uplands; north Wales from Flintshire to Anglesey; western Cornwall; and the plateau of Dartmoor. Thus the Bronze Age population was not large, or continuously distributed. But at least the genepools were continuous in time, the population seemed to be expanding, there was more and more contact of groups with each other and with outside accompanying the development of trade, particularly in metals.

There thus probably existed a biological duality of population in Britain at the commencement of the Iron Age. The Iron Age invaders came into the south and east of the country, and once again there appeared a cultural duality. This distribution of the newcomers would have accentuated any genetic distinction from the north and west that survived through Bronze Age times. Some of the Iron Age settlements indicate a mode of life not very different from that of their late Bronze Age predecessors, storing grain and keeping livestock in their farms or villages, often undefended, lying among little fields on river gravels, altogether indicative of a peaceful existence, conducive to a continuing and stable genepool. But the hill forts which begin to appear in large numbers indicate the developing tribal system and tribal wars as the newcomers multiplied in the southeast. The southwest had a somewhat different Iron Age culture, commencing at the beginning of the fourth century B.C., indicating contact with Iberia and Armorica. The main development of this took place in Dorset and Somerset, spreading along the Cotswolds into the midlands. Again the good quality pottery, metal and wooden objects testify to leisure, particularly the beautiful flowing decoration, but again this civilization depended upon military power, for its hill forts are numerous, massive and intricate. There was a third Iron Age culture, whose links are clearly with the Seine valley, which developed in the northeast of Britain, and particularly the east riding of Yorkshire. Here there was an aristocracy of invading warriors, establishing their dominion over a people whose daily life was still characteristically Bronze Age. While then the strong similarities of the three Iron Age cultures, all deriving originally from settlement by newcomers from the continent, probably represents fundamental similarity of descent, there is evidence of the inflow of genes from different areas into these three different parts of Britain. The last of the Iron Age invasions, best known because it led directly to the invasion by Julius Caesar, was that of the Belgae in the first century B.C. who entered the southeast of Britain from Gaul where they were derived from mixture between Iron Age people of the Marne and the Aisne valleys and newcomers from Germany. All previous inhabitants of Britain had occupied areas of primary settlement, the lighter soils, whether on uplands or on river terraces which were naturally drained and unencumbered by heavy woods. The Belgae had the advantage of the additional traditions of the German forest dwellers, accustomed to living in woodland clearings and with an agricultural technique adapted to working heavy soils.

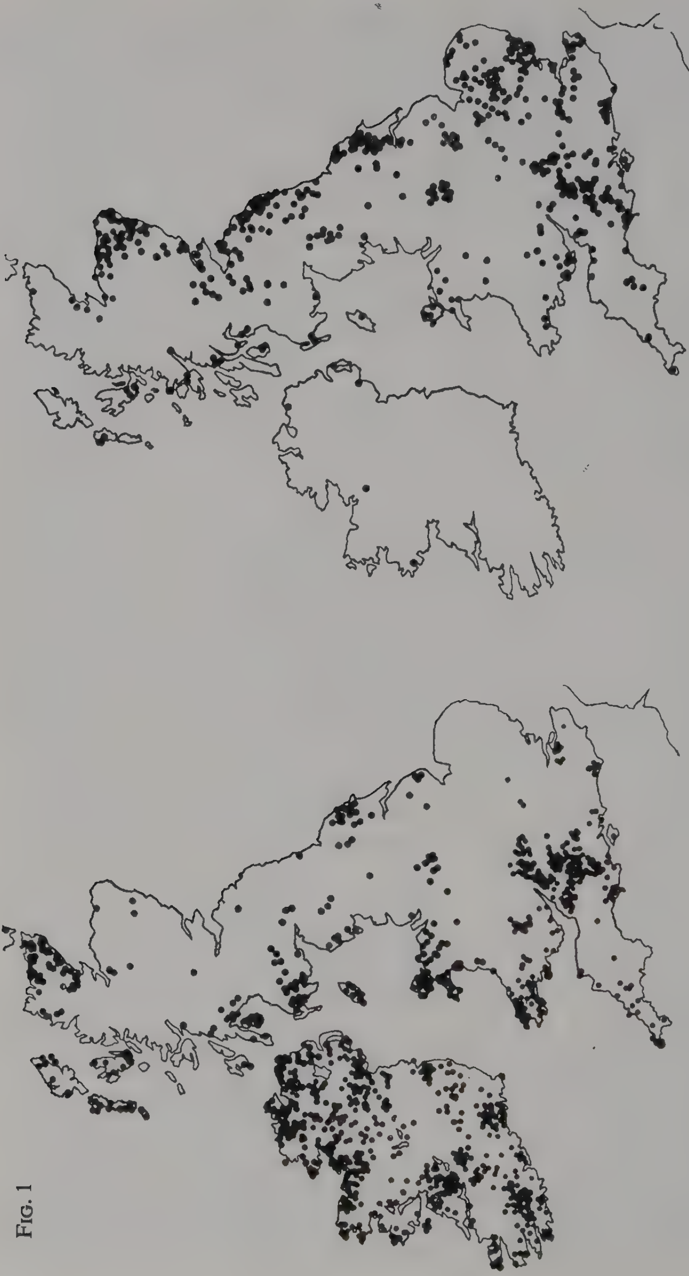
Thus at the time of Julius Caesar in the southeast there was a dense population of vigorous Belgic settlers developing their farms over the countryside, clearing forest, breaking up new land with heavy ploughs, and reaping rich crops. They were divided into small tribes often engaged in petty warfare but they were mainly concerned with pushing forward their own areas of settlement. To the west and north of them and in the forest of the Weald was an older civilization extending to the Wash, the forests of the midlands and the Wiltshire uplands. This was a mixture of primitive Bronze Age with Iron Age culture, a generally stagnant peasant civilization, housed in hut villages, working the lighter soils, its chiefs living in hill forts on the open downs, but with developed larger tribal units, Trinovantes, Iceni, Regni. West of this lay a richer and more progressive people, for the Cotswolds, Somerset, Dorset and the land surrounding them supported a large population of well organized tribesmen, primitive in agriculture compared to the Belgae, but powerful in politics and war, and gifted in the arts. To the northeast there was another culture like theirs, dominating the midland forests from the fortress of Hunsbury. Northeast again were the warriors of Lincolnshire and Yorkshire, who were gradually asserting their supremacy over the hut villages of the northern Bronze Age, and laying the foundations of the kingdom of the Brigantes. Northwards beyond the Clyde were the Caledonians with little contact with the Iron Age folk. The westernmost fringe of the country similarly was in civilization practically untouched by Iron Age influences, though the language may have been acquired. Cornwall was probably the most progressive with its tin trade and ancient connections, but Devonshire, Wales and the northwest were still occupied by a poorer and less-advanced Bronze Age population, living in hut farms and villages with few implements except of wood and stone. The duality of highland (north and west) and lowland (south and east) Britain in population remained, and in the latter at least there was good evidence for some regional differences following the culture zones.

In Roman times the population of Britain numbered perhaps a million mostly in the south and southeast, though there was population increase in the north after the building of Hadrian's Wall. The primary effect of the Roman occupation was the reduction of internal warfare among the various tribes, the development of trade and communications, and improvement of productivity of the land. As the unruly tribes were brought to orderly relationship with one another, undoubtedly many genes of Britons were removed by slaughter, despatch of slaves and prisoners to Rome, service in the legions elsewhere in Europe. There was undoubtedly some inflow of genes from the legionaries of the incoming armies from all over western Europe. But though there was movement of individuals, it is unlikely that the population of Britain moved to any great extent from one part of the country to another. Perhaps there was some movement of genes as people tended to move to the new towns, and in the settlement of the coloniae by the veteran legionaries who were given small parcels of land to farm outside the walls—Colchester, Gloucester, Lincoln, York and others. Most of the people in Britain however still lived in the rural villages, not taking much new land into cultivation from the forest or exploiting the valley bottoms, but concentrating rather on improving the cultivation of the land already occupied, so that great tracts were left uninhabited. Hence it seems likely that, in the districts of the frontier and beyond, the life of the local people was little disturbed, while once the Pax Romana was established the people of the remainder of Britain experienced a period of peace and stability conducive to continuity of the genepool, with relatively little infiltration of new genes, except perhaps in selected localities. The regional differences in genepool of pre-Roman days thus probably persisted.

In the fourth century began a new stream of genes into Britain. Some Picts and Scots were allowed by the Roman government to colonize lands in Britain, but the great invasions of 367 by Picts and Scots on the north and west and by Saxons on the south east heralded the shape of things to come. The first Saxon groups arrived as raiders, later groups came with their families to settle on their chosen piece of land to make it their home. By the middle of the sixth century, Procopius says, Britain was inhabited by three races, Angiloi (=Angles), Frissiones (=Frisians from the coast lands west of the lower Elbe) and Britons. Bede states that the various English peoples of his own day came from three powerful nations, the Saxons, Angles and Jutes. The Jutes included the Cantuari in Kent, and Uictuari in the Isle of Wight and the nearby part of Wessex. The Jutes, from the country east of the lower Rhine, were closely connected with the Saxons. The Saxons, divided into the east, south and west Saxons, came from the countries between Holstein and the Ems, some coming to Britain after being dislodged from Gaul in the fifth century. The Angles gave rise to the East Angles, the Middle Angles, the Northumbrians (i.e. the people living to the north of the river Humber), and other groups. The Angles are mentioned by Tacitus as part of the great confederation of peoples known as the Suevi, and they seem to have reached Britain from Jutland and the neighbouring islands.

In the entrance phase, the infiltration of immigrant groups to the areas of early settlement, penetration tended to be along the rivers, for example Essex and south Suffolk by way of the Blackwater, Colne, Stour and Orwell valleys; West Kent and Surrey by way of the Thames, Medway, Darent and Wandle valleys; Cambridgeshire, Bedfordshire and the valley of the upper Thames by way of the rivers from the Wash. Other penetration was directly inland from the coast as in Sussex and east Kent, north Norfolk. There followed the expansion phase, of secondary colonization around and within the early settled tracts, as well as territorial expansion by conquest. The great Saxon kingdoms emerged. In the final phase the settlement plan filled out and conditions became relatively static. Thus the

FIG. 1

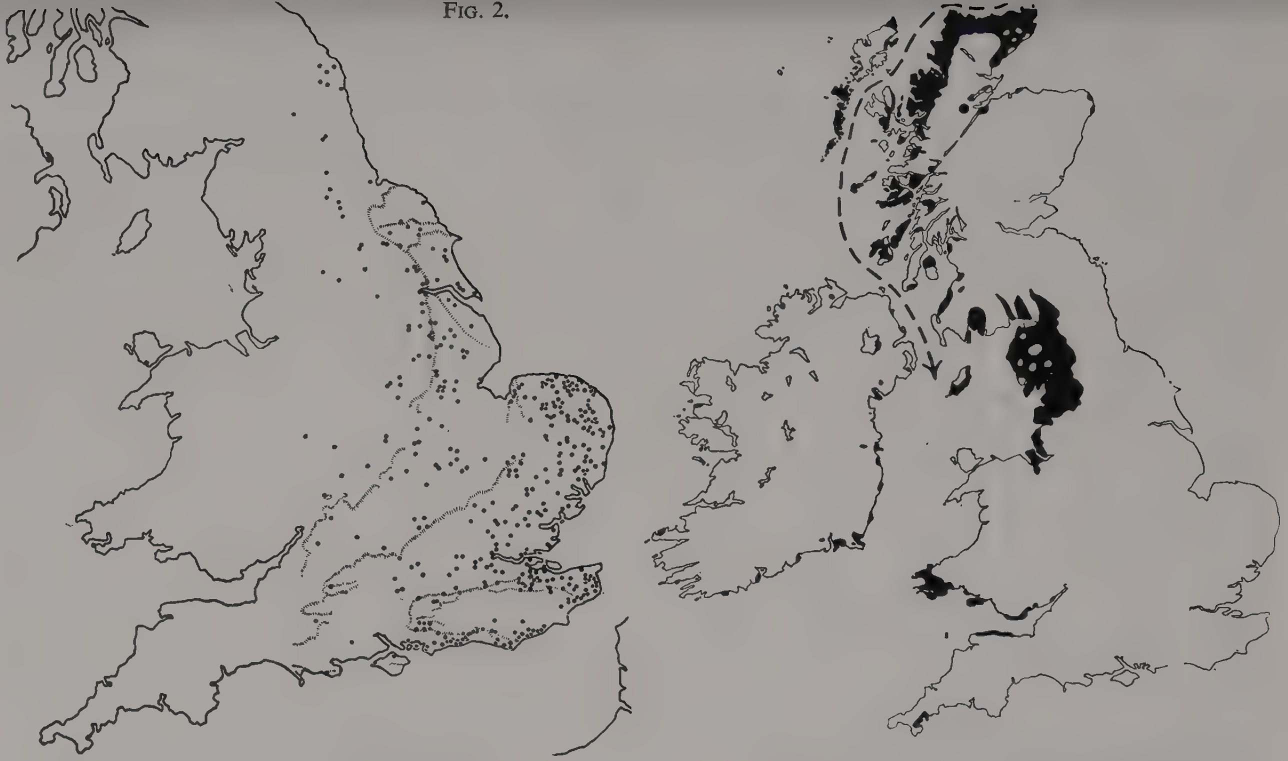


Sites of Megalithic monuments

Sites of beakers—early bronze age

suggest the distributions of their users
(from Fox 1932)

FIG. 2.



Early Anglo-Saxon primary colonization areas

Norse colonization areas

are indicated by place name distributions
(from Wooldridge 1936 and Fleure 1951)

newcomers, entering different parts of the country at different times, may well themselves have differed in their genetic constitution. Their expansion particularly into hitherto unfarmed areas seems to have incorporated a large element of natural increase. In these circumstances the genepool differences amongst the groups of invaders could well have persisted or intensified. Though there were undoubted losses in battle and in massacre at the time of sacking of villages and towns, there is no reason to think that the Romano-British population of any part of England was deliberately exterminated by its conquerors, though their way of life was obviously disturbed. Indeed there is good evidence of continuing side by side existence in many areas, e.g. in Lindsey, where there is a strong suggestion of a British contribution to the royal genealogy at a very early date.

The new populations soon reached sufficient size for genepool stability. For example, in the seventh century the Mercians were a people of some 12,000 households, occupying the whole country from the lower Trent to the forests of the west Midlands. To the north of them, the Pecsaetan consisting of 1200 households were distributed over the Peak district. The Wreocansaetan of the country round the Wrekin comprised some 7000 households. To the southeast of the Mercians, the uplands of central England and the river valleys converging on the Wash were occupied by the middle Angles. Of these the Cilternsaetan, about 4000 households, occupied what is now the Bedfordshire plain; the Gifle, 300 households, were located in south Bedfordshire; the Hicce, also 300 households, were in the locality of Hitchin, the Gyrwe of 1200 households lived on the western edge of the Fens. A distinct group were the Hwicce who occupied what is now Gloucester, Worcester and western Warwick, some 7000 households, who were of mingled Anglian and Saxon derivation. Among other distinct peoples likely to have been characterized by genepool differences were the East Angles, whose local nomenclature points strongly to settlement by a self-contained people whose ancestors had migrated to Britain independently of others, who were subsequently protected by the Fens from domination by Mercia. In Northumbria in the far north, the people known as the Bernice were a formidable enemy to the older northern Celtic kingdoms, and spread over the whole country between the Forth, the Solway and the Tees. A second Northumbrian kingdom, smaller but more ancient, lay in the centre and east of what is now Yorkshire, where a number of Anglian peoples had been settled for more than a century before the year 600. They were known as the Dere, whose first settlements had been along the rivers which converge upon the Humber. Their expansion was long delayed by the British kingdom of Elmet which stretched westwards for many miles from the marshes at the head of the Humber, segregating the Angles of the north from those to the south. Though the Angles of Northumbria and of Mercia were of the same stock, and their dialects closely related, this geographical distinction could well have presaged genetic differentiation. Beyond the northern Britons a small kingdom had been founded in Argyll by settlers from Ireland, whose expeditions reached as far afield as the Orkneys. Throughout Saxon times the peoples of Wales, Scotland and Cornwall remained mainly undisturbed.

Thus on the pre-existing patchwork of genepools that existed in Britain at the end of Roman times, it seems that the Saxon settlements superimposed a second patchwork. Over the generations the genes intermingled, and with the movement of warriors in the many minor battles there was some geneflow between regions. The nature of the settlement gave full scope for genepool differentiation through the founder effect, and subsequently the sizes of the Saxon folk were sufficiently large to maintain characteristic gene frequencies.

The final major stream of gene inflow came from Scandinavia. The same pattern occurred, first raiding, subsequent colonization. At the end of the eighth century, Norwegian adventurers plundered Lindisfarne and Jarrow, but most Norwegian adventurers passed round the north coast of Scotland to Ireland, establishing intermediate colonies in the Shetlands and Orkneys, Caithness, Sutherland and the Hebrides. It was not until the tenth century that any considerable Norwegian settlements were founded in England, as a result of secondary migration from colonies previously established in Ireland. Norwegian colonies were established in the Wirral peninsula, in north Lancashire and along the coast to the south, over much of the Lake District, and into west Yorkshire along the Pennine valleys, and at several points around the coast of Wales. But much more important was the Scandinavian influence in the east, from the Danes. There was little settlement in Northumberland and Durham, except in the south along the Tees. There was widespread influence in Yorkshire, some in Westmorland. But the strongest contribution was in the midlands, in Lincolnshire, Leicestershire, Northamptonshire, some in Nottinghamshire and Derbyshire, and there is evidence that the Lincoln, Leicester and Derby settlements were by different groups. In East Anglia Norfolk was the most widely influenced area. Some clue to the numbers involved is given by the Domesday records, which distinguished the number of sokemen, representing the descendants of the Scandinavian armies which settled. In Lincolnshire the sokemen made up from 20–73 per cent of the peasants, in Leicestershire there were nearly 2000, accounting for 27–50 per cent; in Nottinghamshire 1500. Thus it appears that in some regions the proportion of Danes was equal to or possibly greater than that of the native population. While then there is no doubt that some displacement of the earlier population took place, and the long wars that preceded the Danish settlement killed many people, so that there would be room for much Scandinavian settlement of vacant land, in many cases a Scandinavian leader with his followers merely took over the Lordship from his English predecessor, and there would be little effect on the agricultural population. Again there is good evidence that Scandinavians and English lived side by side in most districts.

Though the Normans shared a common descent with the Scandinavian invaders of Britain, the genes that came in with the Normans were heterogeneous in origin—from Normandy, Brittany, Flanders, central France, Aquitaine, southern Italy. The impact was social rather than genetic, though the social position of the Normans probably enhanced their genetic influence beyond what would have been expected from their numerical proportion. Greater genetic effects probably emanated from the warfare and rapine, and the famines that followed the great devastations, punitive and political, that affected so much of the country, and particularly the north. Many of the known English families became extinct between the coronation of King William and the completion of Domesday, the daughters of others married the Conqueror's barons. But the peasantry, despite their difficulties in a situation where land and resources had been deliberately wasted, were the foundation of the new society, continued to breed and pass on their genes. Again there was probably little mass movement of genes from one part of the country to another. The people of Wales and of Scotland remained relatively little affected.

There has been no episode of great inflow of genes in the last 900 years. Instead over much of the period it has been slight and continuing. There was some effect from the arrival of the Flemings invited by Edward III, the many refugees from the wars of religion of the Continent, the Walloons in Kendal, Norwich and Canterbury, the Jewish immigrants fleeing from continental persecution, the Huguenot refugees in the seventeenth century, Germans in Munster. With the development of trade came many foreign merchants some of whom settled, while many an English trader overseas brought back a spouse and many a prisoner of war contributed. But these probably had little effect on the genepools of the regions as a whole. The most recent wave has been the European refugees and invited immigrants from the Commonwealth of the mid twentieth century, who in turn will make their contributions in particular areas to the richness of the genetic heritage of Britain.

Genetic Implications

The intention of this summary of indirect evidence was to indicate how genetic variation in Britain could have come about. For the earliest periods it is inferred that major rapid cultural innovation over a wide area means at least some new genes, though this is not to embrace the fallacy that all cultural difference necessarily indicates genetic difference. The evidence for later migrations is strong enough to indicate the likely course of events. Apart from the major migrations there was also the slow infiltration of new genes by occasional newcomers from outside, whose effects if any would operate much more locally.

It seems that the initial genetic product of each major pre-Norman immigration can be likened to a chequerboard of genepools, for relatively small founder groups in each invasion occupied different localities, so allowing in each the operation of some founder effect on gene frequency. The subsequent colonizing success and numerical expansion of each allowed the establishment of its characteristic frequencies, though differentiation would have been offset, where there was contact with other similar colonies, by gene exchange through marriage; there was as it were, horizontal interaction across the chequerboard. The succession of immigrations thus gave rise to a succession of chequerboards, superimposed one on another through time. There was therefore ample opportunity for all gradations of interaction between the layers or parts of them (i.e. vertical interaction). At one extreme there may have been complete extermination of the older and replacement by the new, giving perhaps total replacement of genepool, or partial replacement if some indigenes, especially women, remained. At the other there may have been peaceful coexistence (particularly where ways of life or demands on land were not in competition) leading to intermarriage and eventual fusion of genepools. Gene frequencies in the successive waves probably did not differ greatly, apart from the founder effect, since almost all later invaders were from northwest Europe, so perhaps a greater contrast is to be sought between the genetic contributions of the later invaders and those earlier inhabitants of Britain who brought their genes from further south. If so, perhaps those parts of the country relatively little affected by the successive invasions, such as parts of Scotland and Wales, may differ appreciably from the others. At all events the distribution of the immigrant waves suggests that some contrasts may well emerge between northwest and southeast Britain.

But genepools are of course not static. A major process, geneflow between regions, must have been operating in varying degrees of intensity throughout historical time. There is gene diffusion over small distances, locally, by local movement of people, intermarriage. There is gene movement over large distances through the movement of armies and their women, traders, sailors, refugees and others; the depopulation of the Highlands, the Irish influx to England in the nineteenth century, the industrial revolution all produced appreciable geneflow. Even were there to have been absolute distinction between two regions of Britain at some stage in the past, geneflow would have diminished the difference and gradients may well have been established over the intermediate areas. In these gradients the effects of geographic boundaries may perhaps be distinguishable. Other processes of genetic differentiation were also in operation. There may have been some random variation in gene frequencies, particularly amongst the small isolated communities. Selection to meet the harsh circumstances of life that existed throughout most of historic time must have been intense. The demands of selection were not likely to have been uniform—compare the requirements for survival in crowded mediaeval London with those of a fishing community on the south Devon coast or of peasant farmers of the bleak moorlands of the northeast. The selective effects of the plagues which quartered the population, or of the recurrent smallpox and typhus epidemics which assailed each new generation will never be measured. On the whole it seems reasonable to expect that much of the local variation within regions of Britain may well have disappeared as a result of parallel selection, geneflow and other processes, except where barriers to gene flow existed, but the major features of distinction between major regions, and especially the two principal cultural provinces, highland and lowland Britain, may have been so entrenched as to persist and to give rise to gradients between them. Other areas where genepools may persist are perhaps in the regions of refuge, the less accessible and less attractive localities of the north and west, and in those communities where a solid group of invaders established a settlement of sufficient size for genetic stability, and sufficiently remote or unattractive to others that its different gene frequencies remained undiluted by gene flow from outside. By contrast, urban genepools may be in a state of relatively rapid change, as a result of the tendency for newcomers and immigrants to congregate in the towns, which as it were act as buffers to geneflow from outside.

Whether such regional and local differences in gene frequency do occur, and if so whether they represent genepool persistence or are the outcome of some other processes of differentiation, are problems deserving more attention than they have hitherto received. Genetic investigations have centred mainly on the ABO blood groups, in which there have been some classic studies, for example by Morgan Watkin in Wales, Fraser Roberts in the English border counties, well summarized by Mourant (1954). Other blood groups have been investigated in much less detail and there is a dearth of investigations of the more recently discovered characters. The next most comprehensively investigated character is red/green colour blindness, for which data from more than 120,000 naval recruits analysed by Vernon and Straker (1943) showed distinct regionalization, with the lowest gene frequencies along the east coast, high frequencies in the south central and especially southwest areas. Despite the ease of examination there have only been a few local studies of PTC taste testing. The studies in this volume relate to work currently in progress to establish the pattern of genetic variation in Britain and to understand the processes responsible for it.

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FACTORS AFFECTING THE GENETIC STRUCTURE OF POPULATIONS: AN URBAN-RURAL CONTRAST IN BRITAIN

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Increasing attention is being given, not only to the effects of man, especially urban man, on the environments of the world, but also to the effects of these environmental changes themselves, and particularly the highly unnatural ones which have been generated in urban areas, on the human condition. Rightly, concern is mainly focusing on sociological and medical aspects, but, since in every way urban living is so different from the life-styles which have prevailed throughout almost the whole of human evolution, every aspect of the biology of man must be being affected by the new conditions (Boyden, 1970). Many of the consequences may be less obvious and more subtle than at first sight would appear, and any of the biological parameters which depend on the ways human populations are demographically and socially structured are likely to be influenced.

In developed nations, the conditions everywhere are far removed from those prevailing under natural environments, but considerable heterogeneity still exists in life-styles and the way populations are structured. The most striking contrast of this nature concerns urban as compared with rural groups, with the latter still usually organized on a simpler basis than the urban ones and with life-styles that seem to have closer affinity with earlier stages of development. To make comparisons of urban/rural situations can, then, offer insight into the ways human populations have changed and are changing and into the effects of these changes on human biology.

During the past 5 years or so we have been concerned with analysing the population structure of a number of rural villages in the Otmoor region of Oxfordshire (Küchemann *et al.*, 1967, Boyce *et al.*, 1968, Hiorns *et al.*, 1969, Harrison *et al.*, 1970, Boyce *et al.*, 1971, Harrison *et al.*, 1971). Attention has been focused on genetic structure as this is indicated by changing demographic trends. Perforce attention has also been devoted to certain social attributes of the population, since these may profoundly influence the nature of those demographic factors which are of genetic importance. Most of the information has been derived from parish records which offer a time-depth analysis to the present-day situation, and through techniques like record linkage and family reconstitution allow one to examine such genetically important factors as variation in fertility and mortality, and the factors which determine such variation; and spatial movement, assortative marriage, and forms of social mobility. Recently, we have begun to examine comparable records from some of the Oxford City parishes for similar features, especially those connected with movement, and which can be extracted directly from the registers of marriage, and it is our purpose here to compare some of the results which are beginning to emerge from this analysis with those previously obtained from Otmoor. Oxford cannot be regarded as a typical city, if such exists, but in the distribution and density of people and in facets of social relationships it contrasts markedly with the surrounding rural area, and even today life-styles are in some respects very different.

As already indicated, we shall devote our attention mainly to the various forms of movement, spatial and social, which have occurred in the rural and urban groups. Movement, particularly that which determines the relationship between where an individual receives his genes and where he passes them on to the next generation, is one of the most important factors determining the genetic structure of a population (Harrison and Boyce, 1972). As yet much of the parish register material we have extracted for Oxford City has not been analysed, but we have been able to obtain some of the simpler measures of mobility for two large and contrasting parishes: St. Giles, which is near the centre of the city and is today practically entirely residential; and the much newer Cowley St. John, which was only established as an ecclesiastical parish in 1883 and which is close by the industrial development to the east of the River Cherwell.

As will become evident, social factors, especially those relating to occupation and social class, are both directly and indirectly of importance in considering population structure and movement, and from 1837 onwards, marriage registers contain information on the occupation of grooms, grooms' fathers and brides' fathers, and brides themselves when they were employed at the time of their marriage. Admittedly this information is not always stated with the precision one would wish and, particularly in the urban situation, is liable to misinterpretation, but in most cases it does seem possible to translate with reasonable accuracy the marriage register record of occupation to that of social class—perhaps the most important substructure of genetic importance—using the occupational keys provided by the Registrar General.

Both in the rural and city areas demographic and social changes have occurred since 1837 and the data on movement, when analysed in ten-year periods, for instance, tend to show marked temporal trends. These data, however, although of no small magnitude themselves (the records for Cowley St. John, for instance, relate to over 4000 marriages), when broken down into the various categories are insufficient to allow detailed examination of the historical changes. It was, however, thought desirable to examine patterns of the last century separately from those of the present, especially since the increasing provision of mechanical transport might be thought to have profound effects on spatial movement, and increasing industrialization of Oxford City must have radically changed the patterns of occupational status. The data have therefore been analysed (for both rural and urban groups) on the basis of two historical periods, 1837–1900, and referred to as early, and 1901–1970, termed late. It may be noted here that the data for Cowley St. John for the early period are not only very limited, since the parish was only established in 1883, but also refer only to the situation just prior to the turn of the century and are therefore not strictly comparable with those from the other areas. Further, St. Giles parish has been subject to some boundary changes, in 1863, 1869 and 1905, which themselves will have affected its social composition.

Results

The information provided by marriage registers on spatial movement can conveniently be referred to as marital movement, but it is important to remember that it refers to places of residence of the two spouses at the time of their marriage and not to birthplaces. Comparison of the parish register records in Otmoor with census data which cite birthplace does suggest a high level of correspondence between average residential distances and birthplace distances, but we do not yet know the situation for Oxford City, where one might expect the relationship to be much less exact. Using place of residence is likely to underestimate rather than overestimate the distance apart of birthplaces. However, it provides information of interest in relation to those aspects of an individual's mobility which lead to the finding of a marriage partner.

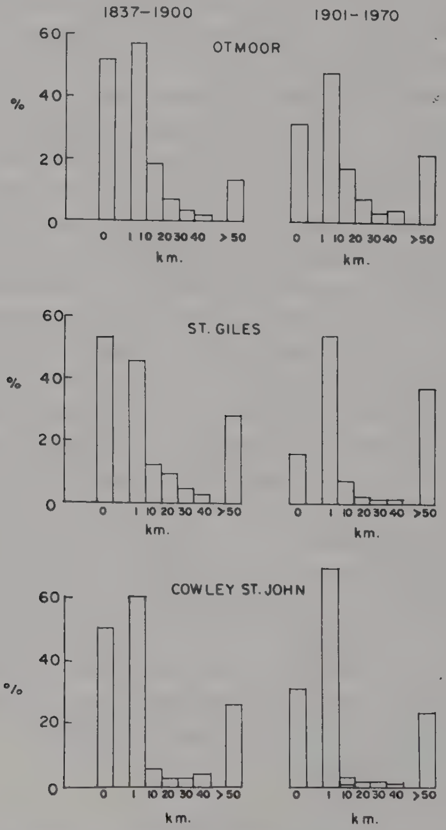

FIG. 1. Distributions of Marriage Distance in Otmoor, Oxford City—St. Giles and Oxford City—Cowley St. John, from 1837–1900 and from 1901–1970.

The distributions of marital distance for Otmoor and the two city parishes in the early and late periods are shown in Fig. 1. Here, partly for scale purposes, a group of marriages termed "endogamous" have been recognized, in which the marital distance is taken as zero. In the case of Otmoor these refer to the cases where both groom and bride were resident in the same parish at the time of their marriage. (The Otmoor data overall is made up of records from eight such parishes.) In the case of the City it refers to cases where the two partners were resident in the same ordnance survey grid square as the church in which they were married. That proportion of marriages which by these definitions was not endogamous, and is therefore termed "exogamous" is then shown as a further proportion of the total exogamous fraction who were living at various distances apart at the time of their marriage.

There are clearly some marked temporal and regional differences. In Otmoor, parish endogamy declines with time, and more marriages are contracted over a greater distance than 50 kilometres in the late period than the early one. Local exogamy tends, however, to follow a similar pattern before and after 1900, and shows the typical exponential decline in marriage frequencies with distance found in other rural populations (cf. Cavalli-Sforza and Bodmer, 1971). The distributions for the two city parishes, especially those for Cowley St. John, are in some contrast. The frequencies of cases in which at the time of marriage both partners were resident in the same ordnance survey grid square as the church in which they were married are very high in the early period—greater than parish endogamy in Otmoor—and fall very dramatically with time—especially in St. Giles. This is no doubt largely due to the expansion of Oxford City, and the concomitant increase in the number of potential marriage partners resident in other ordnance survey squares. More interesting is the pattern of the distribution of exogamous marriages. A much larger proportion of these are contracted either over very short distances (i.e., within the city), or over distances greater than 50 kilometres than in the country. Admittedly, apart from the higher proportion of long-distance marriages, the distribution of marital distance in the early period of St. Giles is broadly comparable with the Otmoor situation, but in the late period, and in Cowley St. John at all times, the marriage records contain relatively very few entries of marriages between city dwellers and people in the surrounding countryside, and the Otmoor records themselves indicate that this is unlikely to be due to a difference in the practice of where the marriage ceremony takes place in short-distance, as compared with long-distance marriages. As shown in Fig. 1, there is no consistent increase in the proportion of the exogamous marriages contracted over 50 kilometres from the early to late period in the city, but this is dependent on the form of presentation, with an endogamous group separately identified: the marked fall in the latter with time must mean that the proportion of marriages contacted outside Oxford City as a whole increases in the late period.

In this analysis we have not taken into account the actual nature of the locality from which a marriage partner from over 50 kilometres away has come, but in view of the nature of the distributions it seems very likely that the majority were resident in other urban areas—none of these of any size occur within 50 kilometres of Oxford. There is thus strong indirect evidence that city-dwellers tend to marry one another, and that there is a reproductive barrier between town and country. Of course, the population density in the city is very much greater than in the surrounding rural areas, and this could largely account for the low frequency of marriages between city-dwellers and countrymen, but the barrier is none the less real for that, and the Otmoor records also show relatively few instances of marriages between people in these parishes and Oxford City. Such a barrier could profoundly affect the distribution of any genes which for one reason or another happened to be at different frequency in the two types of population. Of course, it needs to be remembered that there are other forms of spatial movement than those here attributed to marriage, and there is evidence of extensive migration from Otmoor into Oxford City in the recent past (Boyce *et al.*, 1968).

The nature of the endogamy/exogamy contrasts can be looked at in a slightly different and more easily quantified way in terms of the proportion of marriages which, in the rural area, are contracted within the Otmoor parishes as a whole—Otmoor endogamous—and the proportion of the marriages in the two city parishes which are contracted within the whole of Oxford City—City endogamous. The comparative data are shown in Table 1 and by χ^2 testing are highly heterogeneous for period and locality. This shows, as just inferred, that in the city as well as in the country there is a drop in the amount of local endogamy with time. This analysis, however, also shows quite clearly that in both periods a higher proportion of city parish marriages were contracted in which both partners were resident in Oxford City, than in rural parish marriages where both partners were resident in the Otmoor region, though in terms of area Otmoor is the larger. There are a number of possible reasons for this, including different meanings of the issue of "residence" at the time of marriage in the urban and rural populations, and the doubtless greater proportion of register office marriages in the city. But the situation is likely to be a real one, and a product of the much greater population density in the city. An individual has to cover a much smaller distance to make an equivalent number of meetings with the same number of individuals of the opposite sex in urban conditions than in rural ones.

TABLE 1. Spatial endogamy rates for Otmoor and Oxford City

	1837–1900	1901–1970
Otmoor		
Number of marriages	1171	675
Number of Otmoor endogamous	768	278
Endogamy rate	65%	41%
St. Giles		
Number of marriages	1083	704
Number of City endogamous	778	396
Endogamy rate	72%	56%
Cowley St. John		
Number of marriages	629	3318
Number of City endogamous	491	2444
Endogamy rate	78%	74%

It has been shown in an earlier paper (Harrison *et al.*, 1971) that in the Otmoor area, social class is associated with marital distance, and whilst recognizing that the occupational basis to a social class classification is very different in the urban and rural situations, it seems worth while examining the extent to which social class influences the pattern of marital movement.

The comparative frequencies of the five classes, as established from the occupational status of the brides' fathers, for the Otmoor region as a whole and for the two city parishes, are shown in Fig. 2. It is apparent that there is a considerable heterogeneity according to both period and locality in the frequencies of the social classes, and even the two city groups are divergent. Cowley St. John is characterized since its origin by a high frequency of social class III, as is to be expected from its close association with industrial development.

Although class III also predominates in St. Giles, here there have also been high frequencies of class II, and in the recent period of class I also. Practically all the class I individuals in the three areas are in fact located in this parish, which has been an important residential area for professional people. The Otmoor area, especially in the early period, is characterized by a high frequency of class IV, who are mainly agricultural labourers. Few occupations occur among the Otmoor people, however, which are classified as V. As compared with both the city parishes there has always been a deficiency of class III, particularly in the early period, but class II, composed mainly of farmers, and thus having little counterpart in the city populations, is relatively larger than in Cowley St. John.

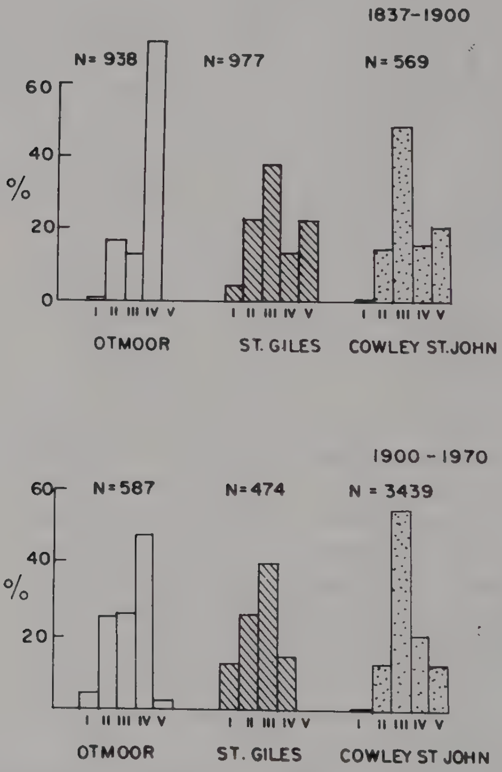

FIG. 2. Distributions of social class in Otmoor, St. Giles, and Cowley St. John as established from the occupation of brides' fathers.

The varying frequencies of the social classes in the different populations contribute to the contrasts in the endogamy rates already mentioned, as can be seen from Table 2 in which the city endogamy rates are compared with the Otmoor ones for the three most frequent social classes, II, III, and IV. Quite marked heterogeneity is manifest here, and a factorial analysis of the data not only indicates significant differences in endogamy according to period locality and class, but also significant interactions between these determinants. Thus, for instance, whereas social class II in the city parishes tends to be less endogamous than classes III and IV, this is not evidenced in the country area with respect to class III in the early period and both classes III and IV in the late. No doubt the fact that the Otmoor class II is largely composed of farmers is responsible for this. It is also evident that the overall greater endogamy in the city parishes is mainly due to the differing behaviours of classes III and IV, especially the former in the early period in urban and rural areas. There is, in fact, less change in the endogamy rate for classes III and IV from the early to late period in St. Giles and Cowley St. John than for these two classes in Otmoor. What is more, whereas class III tends to be highly endogamous in the city, in the rural population the evidence indicates marked mobility on the part of this class in mate selection. This is perhaps the most striking contrast of the analysis. It probably derives from the fact that there are few class III occupations actually being practised in the rural area,

TABLE 2. Spatial endogamy and social class

	1837–1900 Social Class			1901–1970 Social Class		
	II	III	IV	II	III	IV
Otmoor						
Number of marriages	195	139	826	164	169	314
Number Otmoor endogamous	106	76	584	72	61	136
Endogamy rate	54%	55%	71%	44%	36%	43%
St. Giles						
Number of marriages	225	376	134	157	247	91
Number City endogamous	137	282	105	77	151	59
Endogamy rate	61%	75%	78%	49%	61%	65%
Cowley St. John						
Number of marriages	85	279	94	346	1497	595
Number City engamous	57	212	81	214	1098	441
Endogamy rate	67%	76%	86%	62%	74%	74%

and that men of this class are moving out of the area for their daily work. The social class distributions have been established from the occupation of brides' fathers since with the usual English habit of a bride being married in her own parish, brides' fathers give the most accurate estimation of a population's occupational characteristics, but if a father is daily moving considerable distances to work, it seems likely that even if his daughters are not doing likewise, they are being brought into contact with men of a wider area than the daughters of men who are working near their place of residence.

So far we have been concerned with social class as a determinant of population structure through its effect on spatial movement. However, the fact that populations which, though geographically unitary, are subdivided into classes which are to some extent reproductively separated from one another, makes class an important component of structure as well as a determinant of it; and as a component of structure it can have considerable genetic significance, particularly as it affects population breeding size and vertical stratification.

The levels of reproductive separation between classes can be seen as positive assortative marriage for class: levels of assortative marriage thus being viewed as equivalent to levels of endogamy in the spatial context and without any necessary genetic implication. The assortative marriage for class, of course, is not exact, and the cases where partners differ in class can be seen as a form of movement between subpopulations. Movement between populations leads to the development of common ancestry and genetic similarity between them, if it is not itself selective for ancestry and genes. The overall effect of movement can then, as has been shown by Hiorns *et al.*, 1969, be measured in terms of the way relatedness develops between populations which are exchanging with one another and the length of time it takes (in generations) to move from one state of relatedness (usually taken as zero) to another (taken as the state where 95 per cent of ancestors are shared). When this approach is applied to the effects of movement between social classes through marriage, the patterns in which relatedness develops in the Otmoor populations and and in the two Oxford City parishes are shown in Fig. 3 for both early and late periods. There appears to be no systematic urban/rural contrast in these patterns, though those for St. Giles and Cowley St. John tend, in each period, to resemble each other more than either does with those for Otmoor. It may be noted, for instance, that prior to 1900 in the city, and in contrast with the rural group, classes I and II do not develop relatedness with one another relatively quickly as compared with the other classes, and indeed class I, both in St. Giles and Cowley St. John, tends to be more reproductively isolated from class II than class II is from classes III and IV.

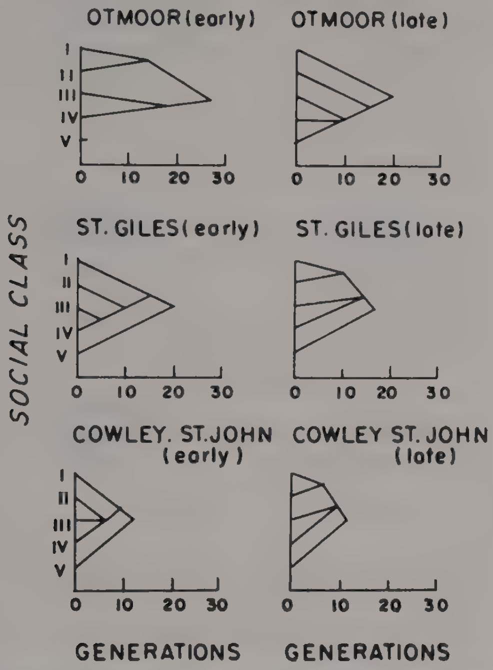

FIG. 3. Patterns by which relatedness between the social classes develops as a result of marriage between individuals of different social class.

In the later period, however, the situation is reversed and it is in the country area that this pattern is found; in the city, classes I and II develop relatedness relatively quickly. To all intents and purposes, occupations ascribable to class V do not occur in the country in the early period, and when they appear in the later one it is evident that the marriage barrier between class V and classes IV and III is not a marked one. By contrast, in both city parishes and both periods, the effect of the marriage behaviour for social class is, relatively, to isolate class V. Indeed, in each of the four cases, class IV comes to be 95 per cent related with all the other classes, including class I, before it develops the same level of relatedness with class V.

Social mobility, in which a child acquires an occupation attributable to a different social class from that of his parents, represents another form of movement between classes, and its effects on relatedness can be examined in the same way as those of marriage.

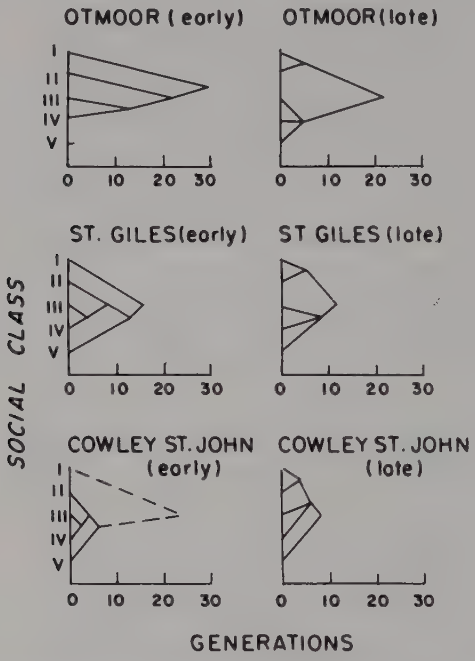

FIG. 4. Patterns by which relatedness between the social classes develops as a result of social mobility.

As already mentioned, parish registers of marriage provide information on groom's and groom's father's occupation. Because the class of father and son is being established when they are of different ages, some biases exist in the data. There are different ways of correcting for this, and not all produce exactly the same results. This, however, is not an appropriate occasion to discuss them, and, in the main, the same general patterns seem to emerge whatever the treatment. With a simple correction which makes social mobility "conserving", i.e. with upwards movement equal to downwards movement, the patterns of developing relatedness between the social classes in Otmoor and Oxford City are shown in Fig. 4. On the whole, and especially in the two city parishes, the patterns produced by social mobility are very like those caused by marriage behaviour. The patterns for Cowley St. John in the later period are practically identical and the difference in the early period is probably due to the very limited data for class I. In Otmoor, however, the social mobility effect in the early period tends to produce a pattern like marriage in the late one, and the social mobility effect in the late period is more like marriage in the early one. This is especially noticeable with respect to classes I and II which cluster together rapidly in the late period but not in the early one. It should, however, be remembered that class I has never been very frequent in the rural area and most of the people in it are not indigenous to the region.

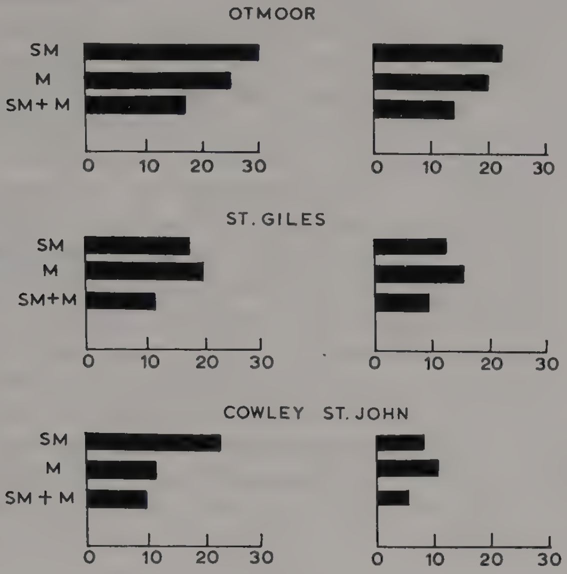

FIG. 5. Number of generations needed to bring the social classes to ancestral homogeneity (95 per cent relatedness) as a result of social mobility (S.M.), marriage (M.) and the two movements combined (S.M. and M.), assuming non-selective movement.

So far, in considering both marriage and social mobility effects, attention has been focused on the patterns by which relatedness develops rather than on the lengths of time involved. The latter, however, which indicates the overall magnitude of the movement, shows some interesting differences between the populations of the three localities, as is evidenced in Fig. 5. Here the number of generations required to establish a 95 per cent level of relatedness between all five social classes are shown on the basis of the effects of social mobility, the effects of marriage, and the combined effects of both movements. There is evidently a marked time effect and both social mobility and marriage are more homogenizing in the late period than the early one, in all three areas. The effect of the two forces, however, appears to show an urban/rural difference. Thus in the city parishes the social mobility is more homogenizing than the marriage effect in three of the four analyses: the exception being Cowley St. John in the early period when the records are limited in number for social class I, which causes the long social mobility effect (cf. Fig. 4). By contrast, in this analysis in both periods in Otmoor, social movement through marriage is greater than that through social mobility. It should be noted, however, that this finding for Otmoor is at variance with an earlier one (Harrison *et al.*, 1970) using less data and a different "age correction", and further information and refinements are required before one can definitely conclude that in Otmoor marriage acts as less of a barrier to movement than parental occupation. What, however, does seem certain, is that in both periods there is overall much less movement between the social classes in the rural area than in the city.

Conclusion

It would be dangerous to generalize far from this analysis, and it is quite possible that even other rural Oxfordshire areas and other Oxford City parishes would show variant patterns. But some considerable urban/rural differences have emerged, and at least aspects of these may have wide occurrence. In this connection it may be noted that some of the distinctive features of both country and city, in this study, seem as evident in the nineteenth century as in the twentieth, despite considerable temporal variation in other features. Thus, for instance, the social class frequencies in Otmoor in the nineteenth century are very different from those in the twentieth, and it has been shown that marital distance is a function of class. Nevertheless, the distributions of marital distance in the country populations, in the two time periods, appear more similar to one another than they are to any of the city patterns. This suggests that one may be dealing here with a rather general phenomenon of urban/rural difference and not something which is merely idiosyncratic to the particular area.

In addition to this overall marital difference phenomenon the study has also revealed contrasts between the urban and rural groups in the nature and magnitude of vertical movement between the social classes through social mobility and marriage. In the rural groups the barriers are stronger and people are less vertically mobile, and this no doubt is also a general phenomenon. Nevertheless, it is apparent that, even in this group, there is sufficient exchange between the classes to allow their rapid convergence for ancestry and genetic constitution, however heterogeneous they may originally have been. Whether or not such convergence occurs depends, as already stated, on whether or not the movement is selective for ancestry and genes. All that the analysis of relatedness provides is a measure of the size of the flow of the channel, not of the nature of what flows along it. One might well expect vertical movement to be selective for those genetic systems which are of occupational and social relevance, and whilst non-selective flow homogenizes, selective flow produces class stratifications in the frequency of the genes involved. Other things being equal, then, the greater flow in the city populations could lead to a greater genetic stratification than occurs in the country! This, however, depends upon many other factors, such as initial levels of heterogeneity, and whether or not an equilibrium level has been reached, which themselves are affected by the nature of the genetic system and heritability levels (Kempton, 1971). About these we can, as yet, say nothing with respect to the Oxford situation, but this analysis has shown that in considering the genetic structure of any population phenomena such as class must be taken into account. If nothing else, they afford insight into what in reality constitutes the breeding population, and there seems little doubt that this varies in rural, as compared with urban situations in developed societies like Britain.

Acknowledgements

Our thanks are due to Miss Christina Freeman, Mrs. P. J. Carrivick and Mrs. N. C. Amery for invaluable help in the computation. We are also grateful to the Nuffield Foundation for a grant which enabled us to study the Otmoor Parishes and to the Social Science Research Council, which is supporting the work on Oxford City.

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MARRIAGE MOVEMENT IN BRITISH CITIES

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With a few notable exceptions populations living in modern towns and cities have received little attention from students of population genetics. Almost all work on marriage movement has been carried out on agricultural communities living in villages of small population size.

These settlements have many advantages for genetical study. In rural communities the economic unit, the social community, the demographic population and to a certain extent the Mendelian population can all plausibly be considered to include the same people in the same circumscribed area. Clusters of small populations, in which each unit is separated from the others by areas of sparse population, can be made to correspond reasonably well with some of the mathematical models which have been proposed to describe gene flow. The permanence of conditions in relatively immobile isolated, small populations makes them valuable for the study of genetics in an evolutionary context, especially where records are available over a few hundred years.

Studies of modern cities and towns seem to promise much less intrinsic genetic interest and much more difficulty. Towns have grown not only through their own natural increase but also through massive migration, from all parts of the country, so that their populations are highly cosmopolitan and between themselves probably exhibit little genetical differentiation. Furthermore their large and continuously distributed populations may be difficult to resolve into communities, either from the point of view of social intercourse or of genetical exchange. Lack of geographical barriers to movement within the city make it difficult to see how such communities are to be delimited, except on class lines, although much sociological evidence suggests that the social activities of some people at least is relatively circumscribed within the city. Lastly the mobility of city populations, and the constant growth which cities exhibit, destroy any continuity of settlement pattern, as for example the more central residential areas are taken over for commercial use. Hence, parishes and other stable centres for which records may be accumulated can be of comparatively short duration. Consequently very few studies have been published of marriage movement in cities with genetical problems in mind. One example is Spuhler and Clark's (1961) study of the breeding population of Ann Arbor, Michigan.

It seems a great pity to ignore the genetics of the predominant part of the population. In England and Wales, more than 80 per cent of the people live in towns and cities, and 37 per cent live in conurbations of a million or more inhabitants. A high level of urbanization is no new development in Britain. By 1850 40 per cent of the population lived in towns of 10,000 people and more, in 1800 21 per cent did so (Jones 1966). Furthermore at the first Census in 1801 London alone had 818,000 inhabitants—about a tenth of the country's population. Admittedly the urban population was proportionately much smaller before the sixteenth and seventeenth centuries, and could not be claimed to have any permanent existence before the twelth century in this country. Nevertheless for eight centuries city dwellers have been a major component of the people, and there can be no doubt that city life is the pattern of the future.

The purpose of this paper is to describe some simple data pertaining to marriage-movement in modern British cities, in order to provide a background against which further studies can be planned. First it may be useful to look briefly at some of the work by non-geneticists on urban marriage patterns, which may be relevant for comparative purposes.

Sociologists are interested in marriage distance as an indicator of the extent of migration, the range of social activities, and the degree of integration or dispersal of communities. American sociologists have been the pioneers in this kind of study. The method is straightforward: records of marriages which took place in a city over a period of a year or two are analysed for the distance separating the partners' residences at the time of marriage. Little further data are available from these records apart from the partners' ages, though some studies have included information about the social class of the husbands. Studies based on such marriage record data can be rather misleading, because they tend to under-estimate the distance separating the spouses at the time when they first met, and therefore of the distance separating the families or communities which are being linked by the marriage. This is because people tend to move geographically nearer to each other from the time of their first date to their marriage. For example, Clarke (1952) in his 1950 study of marriage distance in the city of Columbus, Ohio, found that while 30 per cent of his sample lived within a half mile of each other when they applied for a marriage licence, only 25 per cent of the same sample lived within this distance when they first met. In this country, using the same survey that I have analysed, Friedlander and Roshier (1966) showed that between first meeting and subsequent marriage, in 9·3 per cent of all cases the husband had moved to his future wife's Local Authority area, while in 10·7 per cent of cases the wife had moved to her future husband's Local Authority area. In 71·4 per cent of cases both partners were living in the same LA area when they first met and when they married.

These studies are not of any direct use for genetical purposes because the data do not include the birthplaces either of the partners

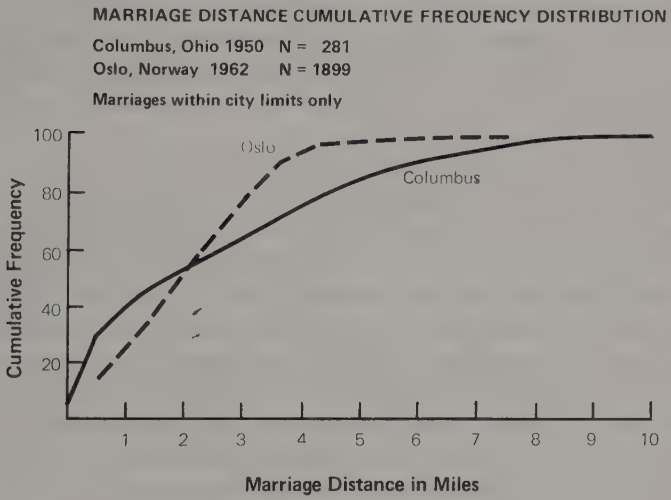


FIG. 1

themselves or of their parents. Nevertheless, they are of general genetical interest because they indicate the range at which mate-seeking activity is being successful.

Most of the studies provide rather similar patterns of marriage-distance. Figure 1 shows a cumulative frequency distribution of data from Columbus, Ohio (Clarke 1952) and from Oslo in Norway (Ramsey 1966). Most of the other American data follow the Columbus pattern rather than the Oslo pattern. However in both cases the median distance is about two miles. Marriages where one partner lived outside the city are not included; they comprised less than 10 per cent of cases.

The Population Investigation Committee Survey

In 1959 the Population Investigation Committee, under the chairmanship of Professor D. V. Glass, carried out a marriage and fertility survey with the aid of the Gallup Poll. Its main purpose was to evaluate changes in people's attitudes and behaviour with respect to family size, contraception, age at marriage and so on. In order to permit regional analysis and migration studies, respondents were asked to state their own and their spouse's birthplaces and place of residence when they first met, together with some information about the circumstances of their first meeting.

The sample was designed to be representative of the whole population of Great Britain south of the Caledonian Canal, aged 16 to 59 inclusive, in 1960. The electoral role was used as a sampling frame. The response rate was 82 per cent, providing about 3000 informants of whom 2338 were married.

The survey does not give enough information to provide the models of genetic exchange described for example, in the Otmoor villages by Kuchemann *et al.* (1967). Because it was a nationwide survey no circumscribed area, with the possible exception of Greater London, provides enough data for rates of exchange between neighbouring places to be calculated. Even a town as big as Sheffield, for example, is represented by only 24 respondents. Parent-offspring distances cannot be calculated because respondents were not asked about the birth places of their parents, and only in some cases can the birth places of the respondents' children be worked out. The survey was not, after all, designed to answer such questions.

Analysis is still in progress. The material to be presented here concerns England and Wales only and, after exclusions, relates to a total of 1639 respondents. Two kinds of information can be extracted relevant to the distance between people who marry:

1. For the total useable sample, the number of marriages where the partners lived in the same local authority area when they first met. I have called such marriages "endogamous".
2. For those partners living in different local authority areas when they first met, the straight line distance separating their places of residence (using a ruler and map), as assessed by the distance between the centre of one local authority area and the centre of the other. For the purposes of this paper, this distance is the "marriage distance".

The cases that were excluded (363) from the material of the original survey were those where one partner claimed to be living abroad when they first met; place names were illegible or untraceable—this caused small villages to be somewhat underrepresented; or one partner was undergoing military service when they first met, for the conditions of service life, in barracks far from the individual's home, would cause the data to be not strictly comparable with those from ordinary civilian communities.

While then the survey can only provide a restricted amount of data for relatively crude analysis, the relative scarcity of this kind of information justifies its presentation, for it may provide useful background for future investigations of the genetical structure of city populations.

Results

(i) Endogamy

In England and Wales as a whole, more than 70 per cent of all marriages were between people who met each other when they were living in the same Local Authority area: that is, the same Civil Parish, Urban District, Municipal Borough, County Borough or Conurbation. The sample includes the complete spectrum of Local Authorities, from the smallest village to Greater London, so if figures for endogamy are to have any meaning they must be related to the population size of the places where the individuals were living. The data are therefore arranged in classes according to the population size of the husband's home town; these classes therefore remain somewhat heterogeneous since each includes a large number of places each of which contributes only a small number of respondents. In Fig. 2 the intervals on the horizontal axis are the class mid-points on a log scale, on the vertical scale is shown the percentage endogamy plus or minus one standard error (vertical lines).

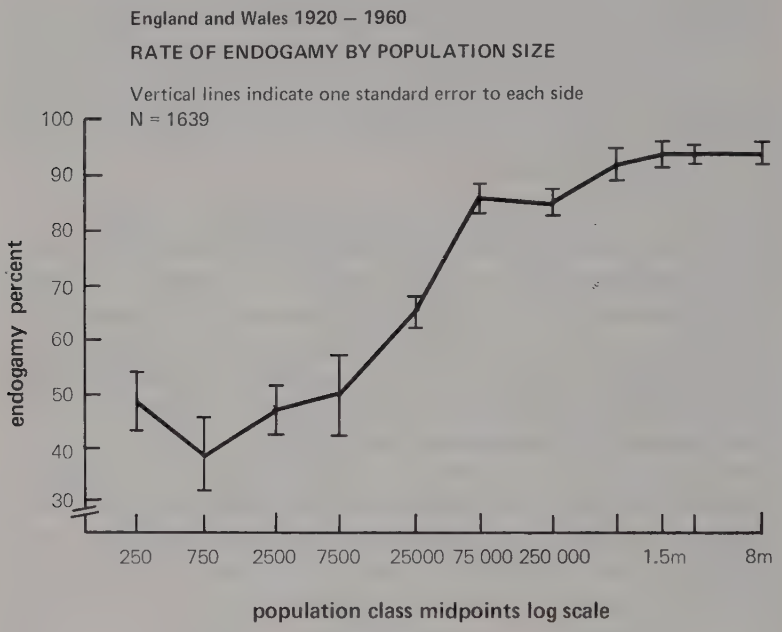


FIG. 2

Predictably, the rate of endogamy rises with population size. Villages and towns with less than 10,000 inhabitants have a fairly constant rate of about 50 per cent endogamous marriages. In towns above that size, the proportion rises rather rapidly so that towns up to 25,000 inhabitants are 65 per cent endogamous and towns over 50,000 inhabitants are more than 80 per cent endogamous. The highest figures are reached by the conurbations at 95 per cent.

Of course as population size and area grows, a "rate of endogamy" tells us less about mate-seeking behaviour. In the larger towns it is quite possible for people to marry who lived two miles apart, and still be ranked among endogamous marriages, because the town will be more than two miles across. Unfortunately the P.I.C. sample cannot throw any light on the problem of exchanges between different communities within the same town.

Conurbations

323 respondents came from the Greater London area, of whom 300 gave sufficient information for their marriages to be analysed by Metropolitan Borough. In 52 per cent of these 300, both partners were living in the same borough when they first met. Now the average population size of the old Metropolitan Boroughs in 1951 was about 115,000 (although the variance was high). But the rate of endogamy of towns of this size outside conurbations is over 80 per cent; so the rate for the London Boroughs is much less than expected. The influence of the population of the surrounding contiguous boroughs is clear, brought about perhaps by factors such as long journeys to work in the London region, the centralization of some entertainments, the well developed transport services.

An interesting contrast is provided by the component boroughs of the other conurbations: Birmingham, Manchester, Merseyside, West Yorkshire and Tyneside. Here, unlike London, there tends to be one very large central "core" borough with a population of half a million or more, like Manchester CB with a 1951 population of 703,000. Scattered around are a number of satellite boroughs with rather smaller populations. Rates of endogamy in the "core" boroughs are predictably high, averaging 94 per cent. In the satellites whose average population, in different conurbations, ranges from 34 to 112,000 (1951), with an overall average of 74,000, the overall rate of endogamy is 76 per cent. But in the main sample the endogamy rates in population classes 25–50,000 and 50–75,000 are 72 per cent and 84 per cent respectively. Hence the rate of endogamy of these conurbation boroughs is similar to that expected if they were independent towns not associated with any conurbation at all. This may indicate a considerable difference in the social, economic and ultimately genetic integration of the different conurbations.

Form of the Relationship between Population Size and Rate of Endogamy

Clearly the relationship between population size and the rate of endogamy is far from linear. It seems to approximate to the form of a logistic curve (this has not been tested). A ten-fold increase in population size, from villages of 500 to towns of 5000 people, leaves the rate of endogamy unchanged at about 50 per cent. The next tenfold increase, from 10,000 to 100,000 inhabitants sees a rapid increase to 65 per cent for towns up to 25,000 population and over 80 per cent for towns over 50,000. Further increases in size do not raise the rate above 95 per cent.

These figures suggest the existence of some kind of threshold in population size, which is crossed when a town has a population somewhere between 10 and 25 thousand inhabitants. Below this figure at least half the inhabitants marry people living elsewhere. Above it, a rapidly increasing proportion find mates within the town's boundaries. The nature of the threshold, if it exists, is not obvious. It may be that a certain population size is needed, for purely economic reasons, to support various facilities which attract temporary or permanent migrants: a wide range of jobs, entertainment facilities, the provision of schools beyond a certain level. Work and play are known to be important in providing opportunities for people to find their future spouses. Pierce's (1963) analysis of these P.I.C. data showed that 15 per cent of married couples met for the first time at work, 27 per cent at dance-halls. Inhabitants of places where these facilities are absent will be drawn outside their town or village to the central places where such facilities may be found. Evidence of a relationship between the population size of a town and its provision of economic and social benefits, which might explain this threshold effect, seems not to exist in any form which lends itself to easy tabulation.

Demographic factors may be important. Considering first the sex ratio, in general, the smaller the settlement, the more unbalanced is the sex ratio with an excess of males. This is particularly pronounced in unmarried people between the ages of 15 and 29. The cause is the wellknown tendency for unmarried females to move from small rural communities to larger urban areas, producing a deficit in the countryside and a surplus in big cities. The data summarized in Table 1 show that the unbalanced sex ratio is not linearly associated with population size. It changes rather slowly between larger urban centres but rapidly reaches extreme proportions in rural districts. It seems reasonable to assume that villages and small towns with an unbalanced sex ratio will have a higher proportion of exogamous marriages because of the intensified competition for mates.

Population density is another demographic variable which may influence the relationship of endogamy rates with population size.

TABLE 1. England and Wales 1951. Sex ratio of people aged 15–29 (Males to 100 Females)

	Rural districts	Urban areas 50,000	Urban areas 50–10,000	Greater London
Single	170	118	113	104
All	124	94	93	87

Source: 1951 Census, General Tables, Table 26, p. 74.

Crude population density is positively associated with population size. For example, in 1951 the population densities associated with various sizes of urban settlement were as in Table 2.

TABLE 2. England and Wales 1951. Population density by population size

London AC	44·7/acre
Birmingham C.B.	21·8/acre
Greater London	18·1/acre
Urban areas >100th	14·2/acre
Urban areas 50–100th	8·5 acre
Urban areas <50th	3·0/acre
Rural districts	0·3/acre

Source: Census 1951, General Tables, Table 8, p. 11.

The rural district figures are misleading because the area includes the countryside as well as the villages; otherwise the general trend is clear. Other things being equal, a more densely crowded population will increase the number of potential mates within a given area.

Comparison with Other Data

A few previous studies have provided isolated sets of data on rates of endogamy. Most are studies of a particular village or group of villages. Of those which provide data pertaining to the P.I.C. survey's time span (effectively 1920–1960), some of the figures for villages do not correspond well. For example, Pons' (1955) study of 11 Hertfordshire parishes gave an average rate of 41 per cent between 1920 and 1940. Williams (1954) found a rate of endogamy of 30 per cent for a Welsh parish (Llandewi-Aberarth) from 1921–1950. Perry (1960) in a study of 27 Dorset ecclesiastical parishes showed that from 1917 to 1936 the average rate of endogamy was just over 30 per cent. Some of these studies, then, give rather lower figures than the P.I.C.

average of 45 per cent for places of less than 1000 inhabitants. Some of the differences may be explained by the small population size of the communities; Williams' Welsh parish had only 354 people, and many of the Dorset parishes investigated by Perry had fewer than 200. Here rates of endogamy for individual villages were highly variable, ranging from 19 to 62 per cent.

Only a few isolated sets of data are available for towns. In her 1951 study of Banbury (population 19,000) Stacey (1960) found that 68 per cent of local born people married other local born people, although these comprised only 32 per cent of all marriages. In Swansea (1951 population 171,000) Rosser and Harris (1965) found that between 1914 and 1960 82 per cent of the residents married within the city limits, 30 per cent of them in their own district. In Aberdeen (1970 population 182,000) a sample of 330 marriages showed that 63 per cent were between partners both born in Aberdeen, and in 90 per cent at least one partner had been born in Aberdeen. This survey was performed by Illsley and Thomas, quoted in Susser and Watson (1962). Lastly, in Bethnal Green, Young and Willmott (1957) found that in 68 per cent of their sample of married people, both partners had been born in Bethnal Green.

Insofar as these figures can be compared with the P.I.C. data, they agree fairly well with the expected relationship between rates of endogamy and population size.

(ii) Marriage Distance

Marriage distance is a much more informative index of marital exchange. Unfortunately in this sample figures are available only for exogamous marriages. Figure 3a shows the frequency distribution of exogamous marriages for marital distances of up to 20 miles using data from all parts of England and Wales except the conurbations, from 1916 to 1960. The sample size here is 256. Figure 3b using larger intervals shows the frequency for all marriages over all distances, to a maximum of more than 100 miles. As previous studies would predict, the distribution is highly skewed. The arithmetic mean is 21 miles, unrealistically inflated by the small number of marriages at very long range. The mode is at 2 miles, the median 5·5 miles.

The endogamous marriages can be brought into the sample to make a combined distribution if we can assume that all marriages classed as endogamous (except those in conurbations) bring together

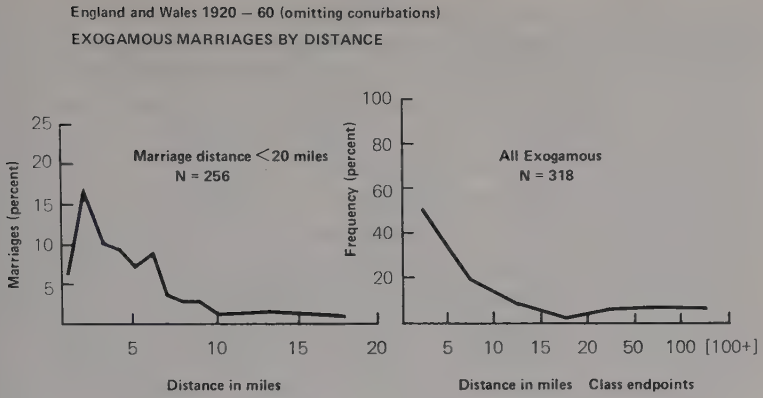


FIG. 3

people living less than 3 miles from each other. This is the approximate diameter of the 20 largest towns in England and Wales. Naturally this combined distribution (Fig. 4) is much more skewed and leptokurtic than the first, in this respect more closely resembling the distributions recorded from previous work. It appears that 76 per cent of marriages in England and Wales between 1916 and 1960

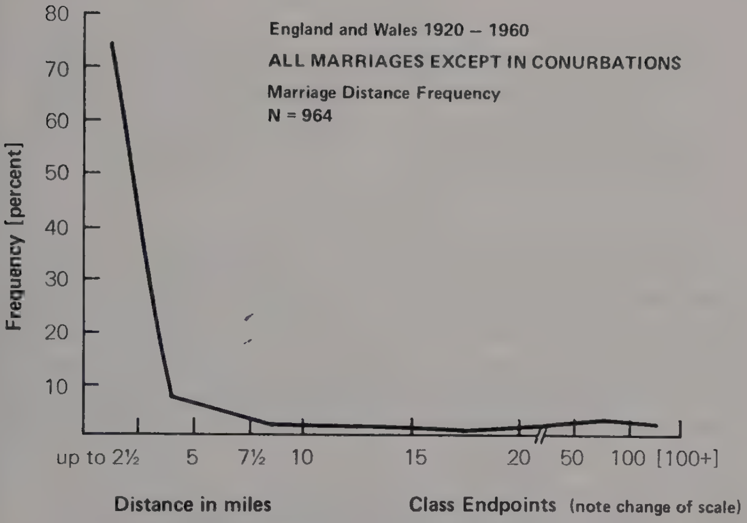
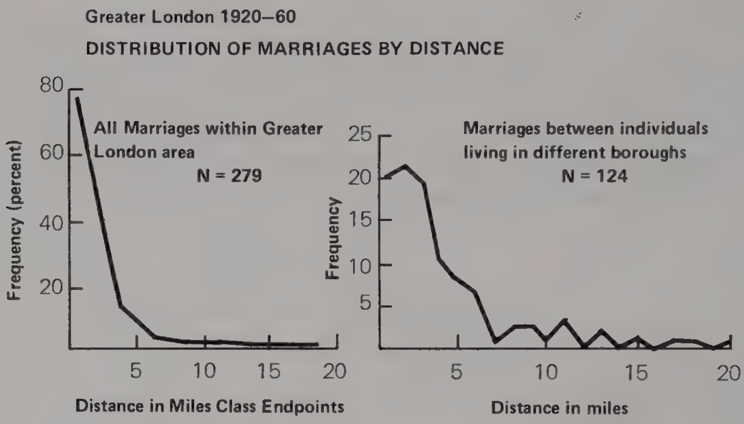


FIG. 4

(outside conurbations) were between people who were living within 2·5 miles of each other; 84 per cent were within 5 miles and 90 per cent within 10 miles. The tail is very long. Forty-three marriages (0·45 per cent) are over 50 miles, and 19 (0·20 per cent) are over 100 miles.

Marriage Distance in Greater London

Because greater London is composed of a large number of boroughs it provides some relatively crude information on marriage distance within an urban agglomeration. Forty-eight per cent of marriages in the London sample were between people living in different boroughs. The distribution of distances between the partners' residences is shown in Fig. 5b. Twenty per cent were within 1 mile, 41 per cent within 2 miles and 79 per cent within 5 miles. The modal distance was 2 miles, the same as for the sample from the towns described above, but the median was only 2·5 miles, less than half. This is hardly surprising, as the great concentration of dense contiguous populations in London will obviously provide many more opportunities for meetings than the sparsely-populated rural hinterland of a smaller town.



Greater London 1920–60

DISTRIBUTION OF MARRIAGES BY DISTANCE

FIG. 5

If we make some assumptions about the size of the London Metropolitan Boroughs, all the data can be brought together in one distribution, as before. Until the introduction of the Greater London

Council and the consequent redefinition of boundaries, the area of the "average" London Metropolitan Borough could be represented by a circle of radius 1·13 miles. Therefore we can say that all the 155 endogamous London marriages brought together individuals living not more than 2·3 miles from each other. Inclusion of these data with the others provides the frequency distribution shown in Fig. 5a. Here 78 per cent of marriages are within 2·5 miles, 91 per cent are within 5 miles, 97 per cent within 10 miles. Obviously both median and mode must be within 2·5 miles. The median is quite similar to those for Oslo 1962 (1·9 miles), Columbus Ohio 1950 (1·7 miles) and Philadelphia 1931 (1·9 miles), but the distribution of distances less so, with London having more at under 2·5 miles. The necessary crudity of the analysis prevents the London distribution from being very informative, for these percentages do not tell us much about the mate-seeking behaviour of Londoners, or the size of the communities involved. A circle of diameter 2·5 miles in central London in 1951 would enclose a population of about 155,000 of whom about 10,000 would be unmarried females aged between 15 and 29. Clearly such a population is much larger than any neighbourhood group linked together by networks of acquaintanceship, within which a proportion of marriages might be expected to take place.

Marriage Distance in Relation to Population Size

There is a marked relationship between the pattern of marriage distance and the population size of the husband's home town. This is shown in Fig. 6.

The distribution of marriage distance in 5 mile intervals for places up to 1000 inhabitants is the highly skewed, J-shaped curve which all previous studies have made very familiar. Almost 70 per cent of marriages are within 5 miles, the median being 4 miles.

The next size of town between 1 and 10 thousand people, has a distribution of similar form but with a noticeable increase in marriages over 5 miles. In marriages outside these small towns, only 50 per cent of marriages are within 5 miles of the husbands' homes; hence the median is 5 miles.

This trend is continued by the marriage distance distribution of towns from 10–100,000 population. Less than 50 per cent marry within 5 miles, the median being 6 miles. There is a corresponding

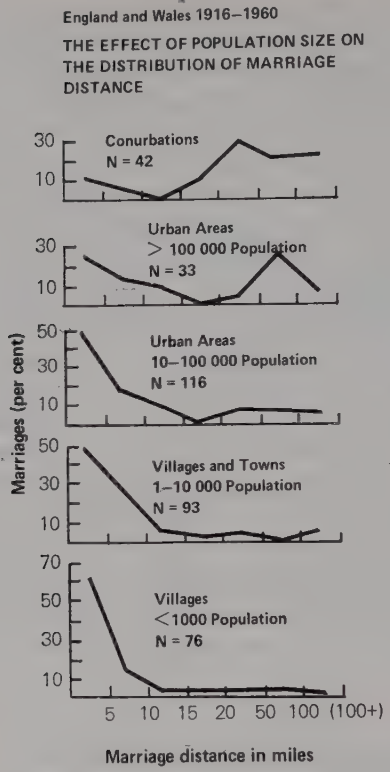


FIG. 6

increase in those marrying beyond 10 miles, especially at long range beyond 50 miles.

In really large towns of more than 100,000 population, the original village pattern begins to be reversed: the proportion of marriages within 5 miles is less than 30 per cent, while an equally large proportion married further than 20 miles from home. The median is between 10 and 15 miles. The sample size here is rather small; only 33. The proportion of all marriages which extend beyond the town boundary is of course declining rapidly with population size.

The reversal of the original pattern is continued further when marriages outside conurbations are considered. Only just over 10 per cent of exogamous marriages are within 5 miles, most being further away than 10 miles. The median is between 20 and 50 miles. Sample size is small (42).

The trend is summarized in Fig. 7 which shows the relationship between the median marriage distance of exogamous marriage and population size of the husband's home town on a log–log scale.

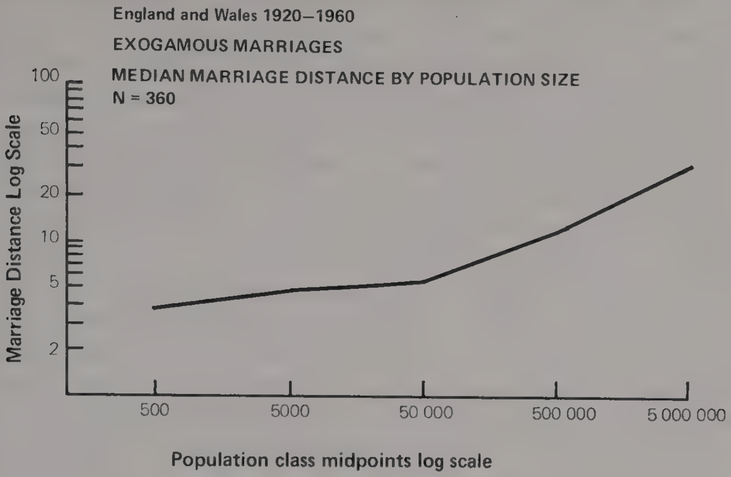


Fig. 7

Reasons for Relationship of Population Size with Distance

What do these changes mean? It is easy to imagine changes in social activity which would lead to median marriage distance rising from 4 to 5 to 6 miles from a man's home town. It seems less easy to understand what is meant in social terms when marriages occur between people whose normal residences are 20, 50 or 100 miles apart. The survey data do not permit a reconstruction of individual case-histories, but it is important to know whether these striking trends reflect real differences in social behaviour (which would have a considerable effect on genetic exchange) or whether they are artefacts. There is, in fact, no evidence to show that the trend is not real, although the mechanism is by no means clear.

Neighbourhood knowledge may be an important factor. It will be related to the length of residence, which in turn will be related to population size. Friedlander and Roshier (1966) have shown using these P.I.C. data that migration of young unmarried people is predominantly away from small rural settlements to larger towns and cities: few move in the opposite direction. Consequently a large proportion of the inhabitants of smaller towns will always have lived there compared to a larger town, where a higher proportion of the population will be immigrants. Therefore it seems reasonable to assume that the inhabitants of smaller towns will be more likely to know other local people, and to be surrounded by relatives and networks of friends through whom potential mates may be met. A lack of such local contacts may well reduce the chances of meeting and marrying someone close at hand. Only a specific local survey could answer this kind of problem.

None of these factors seems quite satisfactory by itself, and a more general explanation is called for. The trend for marriage distance to rise with population size seems to accord well with the expectations arising from geographical central-place theory.

Central place theory is a geographical tool used to analyse the economic and social spheres of influence of towns in relation to their position in a hierarchy of increasing population size. It begins with the basic assumption that a town's size is related to the area of land with which it is connected economically. The larger the area, the larger the town. Furthermore as towns grow bigger they acquire an increasing number and variety of economic and social functions and facilities. A point of interest to us is that several small hinterlands or urban fields, related to a number of small towns, will together support one large dominant town, the "central place", which encloses them all in its hinterland, and so on through several stages.

The larger the settlement, the larger the number of smaller towns and villages it is associated with, and the further apart therefore the average dependent place will be from the central place. Economic connections naturally involve movement from the peripheral places to the centre, for employment, shopping, entertainment and education. The importance of some of these facilities as agencies for marriages has already been mentioned.

For example, in 1947 Corby in Northampton was a relatively small town of 15,000 inhabitants. In 1950 it was designated a New Town and grew to 33,000 by 1959. Though not an ideal illustration because it is unusually dependent on one source of employment (a steelworks) it is useful here because the growth of its urban field has been investigated (Pocock 1960). In 1947 only a few villages were in Corby's urban field; six for example used it for shopping, their mean distance from Corby being 2·9 miles. The hinterland population was very small, estimated at under 800. However by 1959 18 villages were at least partly dependent on Corby for this purpose, with a similar increase for social and educational services. These villages were on average 3·6 miles from Corby, and the urban field was estimated to include about 5000 people.

The long-range marriages in the sample, say beyond 50 miles, cannot easily be explained by changes in a town's urban field. A large proportion, about a third, of these marriages arose from meetings on holiday, a source of only 3 per cent of the marriages in the general sample. Perhaps meetings on holiday can be considered to be the nearest practical approach to random mating within social classes, involving the British population. In this context it is worth keeping in mind that these long-range marriages from holiday meetings are less than a third of all "holiday marriages". A large part of the rest led to marriages between people living in the same town. These, presumably, are the survivors of a number of summer friendships; the others, from different towns, having died of inconvenience. About 16 per cent of the long range meetings took place in the homes of relatives including at least one cousin marriage. Hardly any resulted from meetings at college.

(iii) Trends in Marriage Movement 1916–1960

In order to investigate changes in mate-seeking behaviour over time, the data were analysed into five cohorts, by decade in which the first meeting took place, with the median dates, 1921, 1931, 1941, 1951 and 1961. Except for 1941 these were census years for which population data are available in indexed form. With most analyses, this subdivision produced too many cells for differences to be significant, so larger groupings were used instead: 1916–1945 ("pre-war") and 1946–1960 ("post-war"). The two sub-samples are similar in their proportion of manual to non-manual workers and in the proportions living in towns of different sizes, but in the two post-1935 samples, there is a slight reduction in the proportion of manual workers and an increase in the proportion living in cities. There is a clear trend for the rate of endogamy in each population class to fall with time (shown in Figure 8). The most pronounced changes are in the population classes 0–1000 and 1000–10,000. These are small rural towns and Civil Parishes.

For the most part, trends in marriage distance follow the expected pattern. Median distance in all exogamous marriages was 3·5 miles in the 1920's, 5 miles in the 1930's, 7 miles in the 1940's. For the

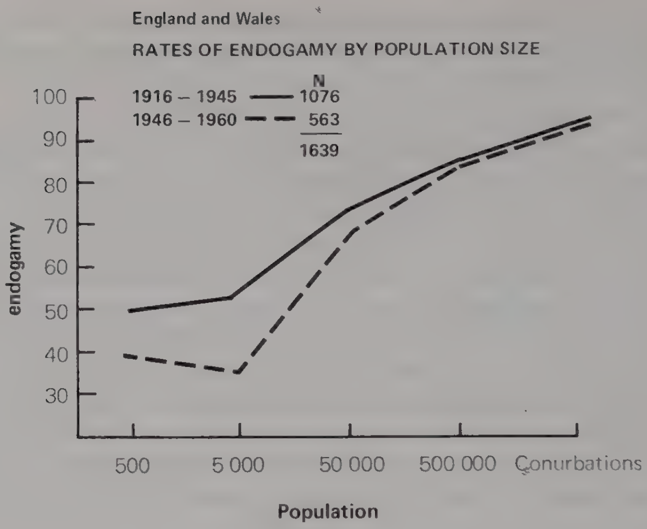


FIG. 8

period 1946–1955 the median slipped back to 5·5 miles but the previous trend is reestablished by the data from 1956 onwards which give a median distance of 7·5 miles, although with a very small sample size (19). The clearest differences in time are those over short

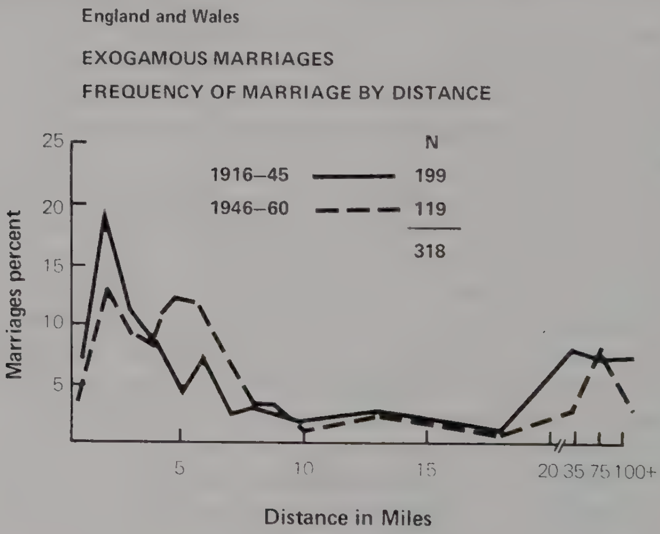


FIG. 9

ranges. Figure 9 shows the data arranged for the pre-war and post-war periods. Pre-war marriages had an obvious peak at 2 miles distance, while after the war marriage distances were more evenly distributed up to 10 miles. The differences in the distributions up to 10 miles distance are significantly different at the 5 per cent level (Kolmogorov-Smirnov 2-sample test, one tail: $\chi^2 = 7 \cdot 6$, d.f. $= 2$.) Numbers are too small for further examination of these trends by population size.

Changes in the Greater London Area

Changes in rates of endogamy and marriage distance are clearly seen in the Greater London area. Up to 1945, 60 per cent married someone from their own borough; after 1945, only 45 per cent did so (significant at the 5 per cent level). This is a much bigger drop than in any of the classes of towns described above. It should be kept in mind that temporal comparisons of London data are complicated by the post-war implementations of the Abercrombie plan which rehoused many Londoners in new towns and peripheral estates, causing considerable reduction in the population size of some east London boroughs.

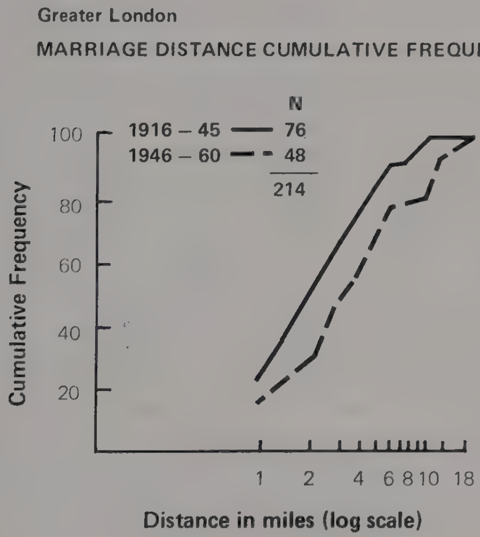


FIG. 10

Changes in the marriage distance distribution in London are shown in a cumulative frequency distribution, in Fig. 10. Significantly more of the later marriages were beyond 2 miles. The trend here is clearer than for the other towns and cities.

Comment on Trends

In general these changes are in the same direction as changes over the same period in migration, length of journey to work, more frequent change of residence, car ownership and others, most of these being related to increased affluence. Some of them are known to be important in the formation of matches; for example about 20 per cent of the sample met for the first time at work, so an increased average journey to work might tend to bring together people from more widely separated communities, and car-ownership will enable people to maintain contact over longer ranges. Relevant statistics are not available for the pre-war years, but individual travel for all purposes is now growing rapidly. For example, in 1953 the average distance travelled per head per day was 6·3 miles, while in 1968 it was 11·9 miles. The projected figure for the year 2000 is 25 miles (Annual Abstract of Statistics).

Demographic factors may account for part of the trend. Population growth by itself, as we have seen above, tends to increase the number of communities brought into the urban field of towns. As this means an increase in the numbers of more distant places brought into regular contact with each other we should expect to see an increase in median marriage distance and a decrease in the rate of endogamy, especially in smaller communities. Population figures for all the different places are, of course, based on the census nearest the time of the partners' first meeting. The factor of population growth is not eliminated thereby, because, as we have seen, the population sizes of nearby settlements may be important in controlling endogamy rates. Changes in the size of nearby communities have not been, and cannot be, taken into consideration.

A slightly less obvious demographic factor is the sex-ratio. It was mentioned before that rural settlements of small population size had very unbalanced sex-ratios compared to larger towns, and that this unbalance was very severe among unmarried people aged 15–29. There have been considerable changes in this imbalance over time, as Table 3 shows. While there has been a general worsening of the sex ratio against males from 1931–1951, it is on rather a small scale.

It is quite insignificant when compared to the very great changes seen here in rural areas. In 1931 the sex-ratio between young unmarried people was 127 males to 100 females. In 1951 it was 170, quite the largest proportional increase in any population class. It is in the rural settlements of course that the greatest reductions in levels of endogamy have taken place.

TABLE 3. England and Wales 1931 and 1951. Single males aged 15–29 to 100 single females aged 15–29

	Rural districts	Urban areas < 50,000	Urban areas 50–100,000	Greater London
1931	127	108	99	96
1951	170	118	113	104

N.B. The urban area classifications used in the two censuses are not strictly comparable.

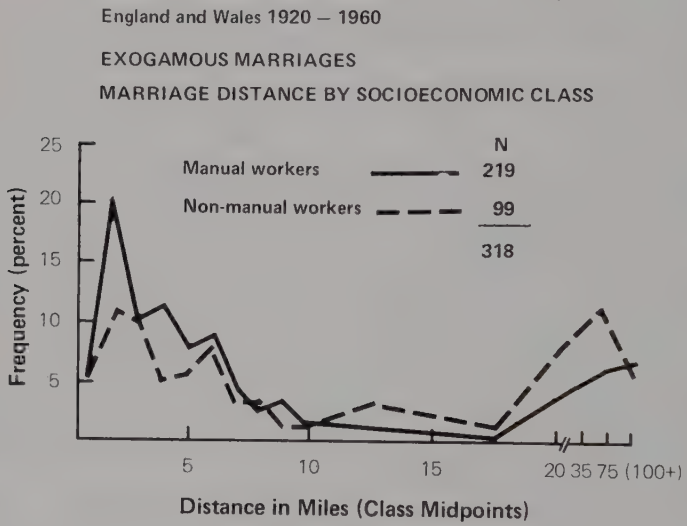
Source: 1931 Census General Tables, Table 19, p. 144. 1951 Census General Tables, Table 26, p. 78. 1951 Census Report on Greater London, Table 21, p. 62.

Lastly it should be pointed out that mere differences in size of towns of themselves would produce different rates of change of endogamy with time. For example; if a general change in social behaviour increased median marriage distance to a mile, then this would mean a large increase in marriages outside small places, but only a small increase in the proportion of marriages outside large places which themselves would be several miles across. This of course is somewhat naive: it assumes that distance outside a town is equivalent to distance within a town, from the point of view of meeting potential mates. Also it ignores the fact that large towns always offer opportunities, unavailable elsewhere, which will lead the inhabitants to marry within its boundaries, whereas this is not the case with smaller settlements.

All these comments merely point out associations between changes in marriage distance and other changes—not real explanations. A specially designed survey is the only effective means of clarifying this problem.

(iv) Analysis by Socio-Occupational Class and Region

The survey data were classified by socio-economic class according to the modified Hall-Jones scale, where classes 1–5 are non-manual workers and classes 6–8 are manual workers. Class 9 is a special residual category. Because of limited sample-size, a two-fold classification into manual and non-manual workers is adopted here. Respondents were classified according to the husband's job at marriage. Seventy per cent were manual, 30 per cent were non-manual. In general non-manual workers marry outside their own home towns more often than manual workers, although the difference is very small. Clearer differences are found in the frequency distribution of marriage distances in exogamous marriages (Fig. 11). The differences between the cumulative distributions is significant at the 1 per cent level. (Kolmogorov-Smirnov 2-sample test, one tail d.f.$=2$, $\chi^2=13\cdot1$.) Non-manual workers are under-represented in marriages within 5 miles of their home town and predominate at greater distances. The median distances are 4·5 and 6·5 miles, for manual and non-manual workers respectively.


England and Wales 1920 — 1960

EXOGAMOUS MARRIAGES

MARRIAGE DISTANCE BY SOCIOECONOMIC CLASS

FIG. 11

This pattern is repeated when the data for Greater London are examined. A clear difference, significant at the 5 per cent level, exists between the proportion marrying beyond 5 miles, the non-manual workers predominating at the greater distance. Such class differences are well known from previous studies and can be attributed at least partly to the possession by the middle classes of a greater share of the affluence whose relation to marriage distance was touched on before. It has been suggested that there may be a greater distance between middle-class enclaves in cities than between the areas which are predominantly working-class so that middle-class marriages are bound to be at a greater distance because of their settlement pattern. The survey did not provide enough data to test this hypothesis.

It was expected that when the data were analysed by different Standard Regions of the country, significant differences might emerge with respect to marriage distance. In fact no significant changes could be detected.

Conclusion and Summary

The intention of this paper has been to provide some background information on marriage distance in cities, and to indicate the areas where research may be profitable from a genetical point of view, especially in the relationship between migrations of genetical interest and social behaviour.

In summary, the proportion of marriages between couples living in the same local authority area rises with population size. But the London conurbation differs both from urban areas in the country as a whole and from other conurbations. The relationship between population size and endogamy is not linear, suggesting the existence of some kind of threshold, above which there is a stronger tendency to marry locally, but demographic factors of sex ratio and population density are also relevant.

Marriage distance shows the usual highly skewed distribution, and again London differs from other urban areas in its greater number of short distance marriages. Again there is a relationship between marriage distance and population size, which agrees well with the predictions of geographical central-place theory.

Marriage movement in the post-war years (1946–1960) is greater than in the pre-war (1916–1945), and the changes appear to be related to affluence and demographic factors. There is also a difference according to occupation, with non-manual workers tending to look farther afield for their spouses than manual.

Many of the findings could have been predicted from extrapolations of genetic investigations of villages and the work of American urban sociologists; for example the relationship of changes in marriage distance to social class, and the changes seen with time. The relationship of marriage distance with population size has not received so much attention.

The heterogeneity of the data has almost certainly prevented differences in analysis from being more clear-cut. For example, when the data are partitioned by socioeconomic class, they are still heterogeneous for population size, geographical region and time, all of which may affect marriage distance. Controlling these variables is difficult, because sample size is thereby reduced excessively. But the work suggests that to obtain useful data on marriage movement in the urban environment, a future enquiry should concentrate on marriages from one town only, and its rural hinterland; it should employ a survey method to extract information not available from marriage records, the sample size being from 1000–2000, and certainly include data on the birthplaces and the migrational and occupational history, of the respondents, their parents and their children. But as much relevant social and demographic information as possible should be collected about the respondents and their town in order to understand the patterns of movement revealed by these data, and to identify class barriers as well as geographical barriers in the urban setting.

Acknowledgements

I should like to thank Professor D. V. Glass and Dr. S. Thapar for their advice in the analysis of the data, Dr. J. Adams for helpful discussions of central place theory, Professor N. A. Barnicot for comments on the finished paper, and Miss S. C. Babington for preparing some of the figures.

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COUSIN MARRIAGE IN IRELAND

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The first report of an attempt to assess the prevalence of consanguineous marriage in Ireland was published by Cameron in 1883 almost a century ago. In 1955 Kilpatrick *et al.* analysed independent evidence from scattered sources to estimate the extent of full-cousin marriage in Northern Ireland. The most recent investigation of consanguinity in Ireland was that of Masterson (1970) using Catholic Church records. In the Catholic Church, marriages between second cousins or more closely related individuals are permitted only in special circumstances and by a dispensation from the Bishop of the diocese in which the marriage is to occur. Records of these provide useful information for the analysis of consanguinity. For the ten year period 1959–68, it was possible on a diocesan basis to obtain data on 190,557 marriages between two Catholics, together with figures for consanguinity dispensations.

The results of this investigation are presented in Table 1. Figure 1 shows the political and diocesan divisions of Ireland with the per cent first cousin marriage rate for each diocesan area. In an attempt to achieve some degree of coincidence between national and diocesan boundaries the combined dioceses of Armagh, Down and Connor, Dromore, Derry and Clogher were taken as being reasonably representative of Northern Ireland whereas the remaining dioceses were deemed to reflect conditions prevailing in the Republic of Ireland. In the latter area, there were 149,029 marriages between Catholics, including 242 first cousin marriages, during the period 1959–68. These figures represent 91 per cent of all marriages and a first cousin marriage rate of 0·16 per cent respectively. In the dioceses representing Northern Ireland there were 41,528 marriages

TABLE 1. Numbers of marriages involving various degrees of consanguinity in the 26 diocesan areas for the 10-year period 1959–68

Archdiocese or diocese	Marriages of two Catholics	Uncle/ niece aunt/ nephew	FC	FC (%)	FCOR	SC	Influence of itinerancy
Armagh	9,134	0	6	0·066	7	20	Not stated
Meath	6,492	0	13 (1)	0·200	0	60	Majority of FC marriages
Ardagh and Clonmacnois	2,822	0	1	0·035	2	25	1 FC, 1 FCOR, 5 SC
Clogher	3,998	0	3 (2)	0·075	0	7	3 FC marriages
Derry	9,275	1	3	0·032	5	27	Not stated
Down and Connor	15,889	0	11	0·069	9	46	Not stated
Dromore	3,232	0	0	0·000	0	13	Not stated
Kilmore	2,580	0	3	0·116	2	14	Not stated
Raphoe	2,800	0	3	0·107	0	19	Not stated
Dublin	59,605	4	72	0·121	6	47	Not stated
Kildare and Leighlin	6,197	0	20	0·323	8	33	Not stated
Ferns	5,344	0	7	0·131	1	23	Not stated
Ossory	3,271	0	3[1]	0·092	0	17	Not stated
Cashel and Emly	3,401	0	19 (2)	0·559	9	27 (2)	9 (1) FC, 2 FCOR, 1 SC
Cloyne	4,677	0	14	0·299	1	19	Not stated
Cork and Ross	13,128	0	9	0·068	0	39	Not stated

TABLE 1 (*Continued*)

Archdiocese or diocese	Marriages of two Catholics	Uncle/ niece aunt/ nephew	FC	FC (%)	FCOR	SC	Influence of itinerancy
Kerry	5,264	0	7 (1)	0·133	3	17	Not stated
Killaloe	4,279	0	6 (1)	0·140	1	19	Not stated
Limerick	7,515	1	14	0·186	6	37 (4)	Not stated
Waterford and Lismore	5,611	0	10	0·178	2	18	Not stated
Tuam	4,785	0	17	0·355	4	55 (4)[2]	Not stated
Achonry	1,337	0	9 (1)	0·673	3	17	9 (1) FC, 2 FCOR, 9 SC
Clonfert	1,379	0	0	0·000	2	8	4 (unspecified) concerned itinerants
Elphin	3,791	0	4	0·105	2	13	Not stated
Galway, Kilmacduagh and Kilfenora	3,408	0	10	0·293	1	36	Not stated
Killala	1,343	0	1	0·074	2	15	Not stated

FC=First cousin. FCOR=First cousin once removed. SC=Second cousin. Figures in brackets indicate double cousin relationship e.g. FC 19 (2)=19 First cousin marriages of which 2 were between double first cousins. SC 27 (2)=27 Second cousin marriages of which 2 were between double second cousins.

[1] Two further dispensations for consanguinity of unstated degree.

[2] In addition to the instances of consanguinity cited here there were 18 marriages between second cousins once removed.

between two Catholics representing 40 per cent of all marriages, with a first cousin marriage rate of only 0·06 per cent.

Consanguinity data for "mixed marriages" solemnized in the Catholic Church in all dioceses during the ten-year period were not

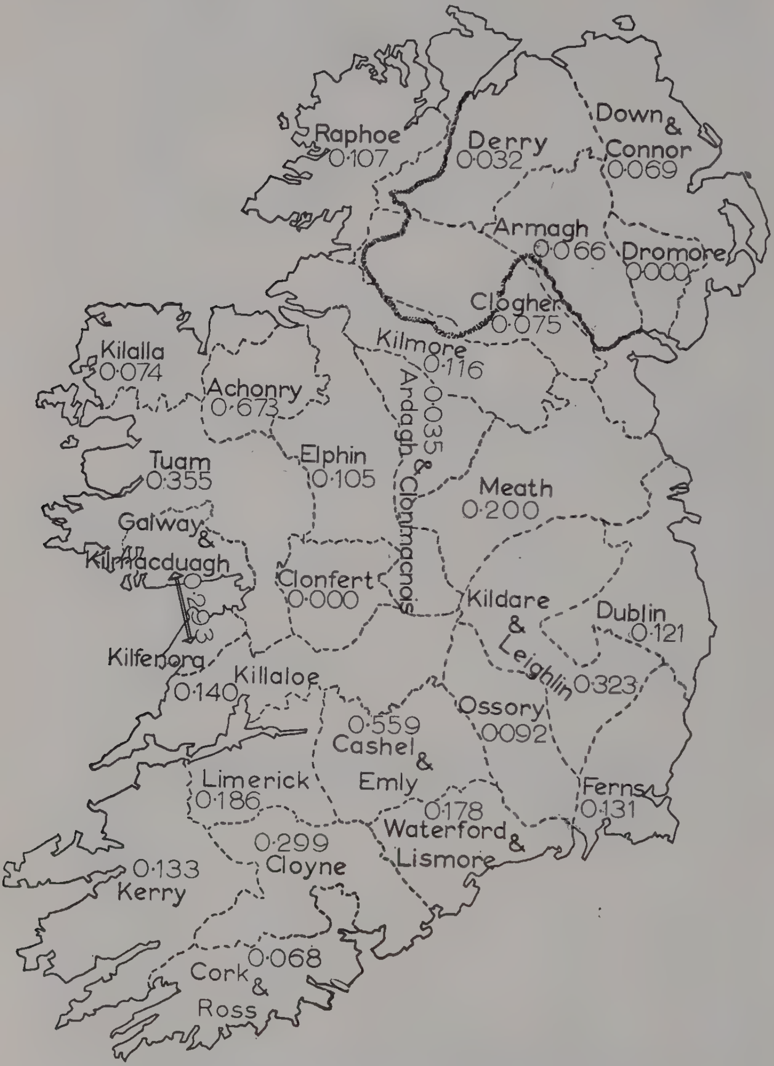

FIG. 1. Map of Ireland showing political and diocesan divisions with per cent first cousin marriage rate for each diocesan area.

sought. Information from the Archdiocese of Dublin, however, showed that in the total 61,250 marriages in the Catholic Church there was no instance of dual dispensation for both consanguinity and religious difference. Figures for 1971 obtained subsequently for the Archdiocese of Dublin and the Diocese of Down and Connor further showed that in 7846 and 2248 marriages in the Catholic Church in these areas respectively, there was not a single instance of dual dispensation. It thus seems that first cousin relationship in "mixed marriages" solemnized in the Catholic Church is extremely rare or non-existent and that the first cousin marriage figures derived only from data on marriages between two Catholics could in fact be reasonably expressed as a percentage of all marriages in the Catholic Church. If this were done the estimates of first cousin marriage rates for the Republic of Ireland (based on 92 per cent of *all* marriages) and for Northern Ireland (based on 42 per cent of *all* marriages) would be very slightly lower than the figures cited above.

Changing social, religious and political influences in Ireland must be considered in assessing the likely trend of consanguineous marriage figures following the period of study 1959–68. Data from that investigation indicated that the itinerants of the Republic of Ireland, who according to the report of the Commission on Itinerancy (1963) numbered 5880 in 1961, were making a disproportionately large contribution to the compiled consanguineous marriage figures. During the past ten years approximately 300 itinerant families have been allotted local government housing and during the past five years a similar number of families have been settled in official sites (Irish Council for Itinerant Settlement 1972). The resultant gradual integration of the itinerant community with the general population should ultimately result in the disappearance of a social isolate in which inbreeding is particularly common. This will in due course effect a significant reduction in the national consanguineous marriage rate. Observations on similar resettlement programmes in the Netherlands and elsewhere, however, suggest that the disappearance of itinerant social identity with its associated tendency to endogamous marriage will be a slow process.

Since the completion of the 1959–68 survey there has been a marked aggravation of religious and political differences in Northern Ireland. It was considered probable that the increasing polarization of Catholic and Protestant communities would lead to a dramatic reduction in the incidence of "mixed marriages" with a resultant increased likelihood of consanguineous marriage within the separated religious communities. It came as a surprise therefore to find that in 1971 in the diocese of Down and Connor, which includes Belfast, the number of "mixed marriages" in the Catholic Church had increased appreciably over the previous year's figures and in fact represented 24 per cent of the total (Table 2).

TABLE 2. Consanguineous and "mixed" marriage data for the Archdiocese of Dublin and the diocese of Down and Connor for 1971.

	Dublin	Down and Connor
Total marriages	7,846	2,248
"Mixed marriages"	345	534
First cousin	7	2
First cousin once removed	2*	3
Second cousin	7	2

* These involved double cousin relationship and in both instances concerned itinerants.

The growth of large urban areas at the cost of rural depopulation is a continuing trend in Ireland and one which is likely to lead to a reduction in the frequency of consanguineous marriage. Thus, between the Census of Population 1966 and that of 1971, while the population of Dublin County Borough remained virtually unchanged, that of Dublin County (which includes the rapidly growing outer suburbs of Dublin City) increased from 175,000 to 231,000. During the same period the combined populations of counties Leitrim, Mayo and Roscommon in the west of Ireland declined from 202,300 to 191,400. Consanguineous marriage data for the Archdiocese of Dublin for 1971 are shown in Table 2. The first cousin marriage rate at 0·115 per cent is marginally lower than that observed for the same Archdiocese in the 1959–68 investigation.

Figures from the ten year study indicated a first cousin marriage rate of approximately 1 in 625 for the Republic of Ireland according to data based on about 91 per cent of all marriages. The corresponding figure for Northern Ireland based on only 40 per cent of all marriages was approximately 1 in 1650. It must be pointed out that these data and the figures subsequently compiled only indicate the incidence of first cousin relationship among Catholic marriages during the relevant period and do not necessarily describe the existing inbreeding level of the whole population. They nevertheless provide a useful index of the extent of a genetically important phenomenon and a yardstick against which trends in subsequent generations can be evaluated.

Acknowledgements

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HISTORICAL POPULATION STRUCTURE IN NORTHUMBERLAND

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In looking for an explanation of present day local gene frequency variation, it is useful to investigate not only the existing population but also their ancestors, since the results of previous migrational, selective or drift events may have persisted to the present day. Investigation of selection in historical populations is difficult, but the possible effects of migration and drift can be more easily approached through the demography of these populations using the plentiful written records which have survived. This contribution will describe some of the ways in which local records have been used to study the genetic structure of historical populations in Northumberland, particularly their size and relative genetic constancy and the degree of genetic isolation between geographically isolated areas.

Materials

The source materials used were transcriptions of the Anglican Church Parish Registers of four ecclesiastical parishes—Alwinton, Rothbury, Felton and Warkworth (Fig. 1). These parishes lie along the valley of the River Coquet. They are markedly different in their geography and so, by reflection, in their social organization. The extremes are Warkworth, lying on the rich coastal plain with a population of 2033 at the 1801 census spread in numerous fishing and lowland farming communities, and Alwinton, deep in the Cheviot Hills with a population of 738 in 1801 scattered over an area more than twice the size of Warkworth.

The registers were, with minor exceptions, complete from 1719, 1653, 1653 and 1679 respectively; earlier registers were probably lost

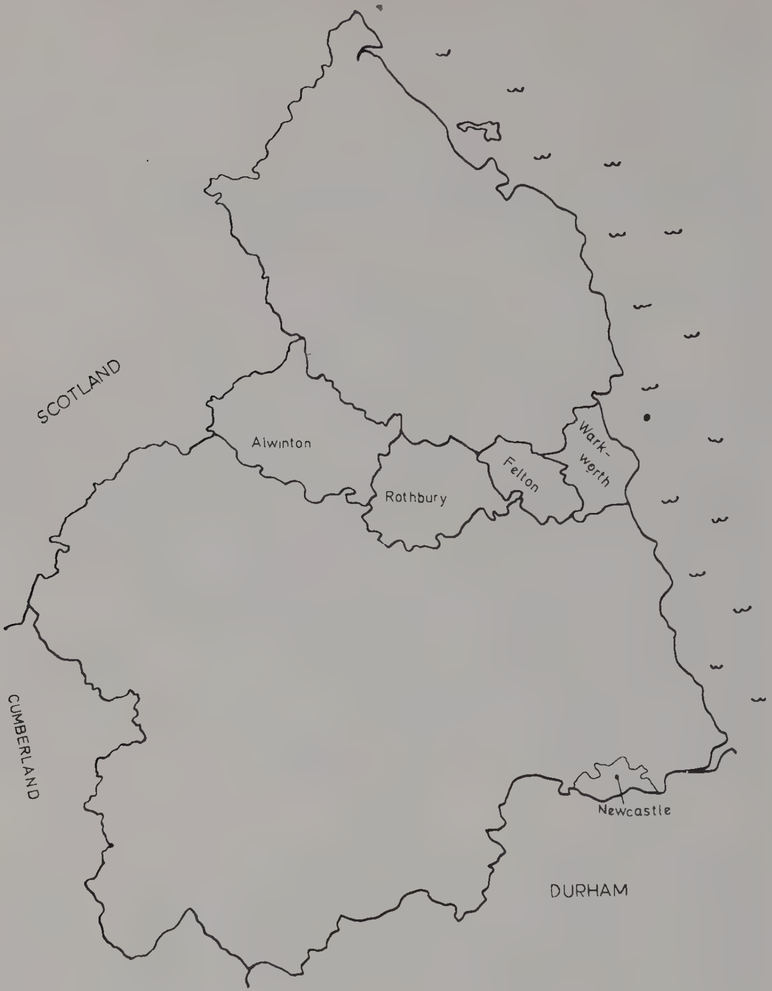

FIG. 1

during the border troubles of the seventeenth century. Use was made of the baptism and marriage entries. Although the exact format changed with time the baptism entries up to approximately 1797 took the general form:

> Date of baptism, christian name of child, sex of child, full name of father, place of residence of family.

After 1797 on the instructions of Bishop Barrington of Durham, the registers in North East England took on a fuller form and contained:

> Date of baptism, date of birth, full name of child, parity and sex of child, full name of father, place of residence and occupation of father, parish and possibly place of birth of the father, full maiden name of the mother and parish of birth of the mother.

This form continued until the Rose Act of 1812 introduced printed registration forms.

Marriage entries were also of two types:

(i) Before the Hardwicke Act of 1753 the entries varied from parish to parish, but the fullest entry gave:

> full name and place of residence of each partner and if one partner came from outside the parish reference was generally made to the fact.

(ii) After the Hardwicke Act the parish of origin was substituted for place of residence.

Methods

Two approaches are available for the use of Parish Registers in this context, either "family reconstruction" or "aggregation" (Wrigley 1966). The former, which entails the reconstruction of multigenerational pedigrees, is the more accurate, but it is extremely laborious and can be applied to only the most complete and detailed records, the present material has proved too limited for "family reconstruction". In the latter method population structure is studied indirectly by assuming a constant relationship to data which can be extracted direct from the records. Using two aggregative methods—surname analysis and marriage distance analysis—a preliminary survey was made of the four parishes to investigate their relative stability.

Surname Analysis

Surnames are, strictly, markers only of the Y chromosome, but in a population they can be used as a general genome marker. Thus the relative constancy of surnames in a population can given an estimate of their relative genetic constancy.

Using the method of Buckatzsch (1951), this type of analysis was carried out on the Northumbrian parishes to estimate the genetic continuity over time. For each parish separately, the total number of different surnames found in the baptismal entries during the 30 year period from 1780–1809 was calculated. The number of these names which also occurred in the preceding series of 30 year period was then calculated. The results are shown in Table 1 and Fig. 2, together with comparable date from Buckatzsch (1951). The bold figures on the diagonals in Table 1 represent the numbers of different surnames found in each 30 year period, and the figures horizontally to the left of the bold figures represent the numbers of these surnames which were also present in the previous 30 year periods. For comparison the figures relating to the latest period are plotted in Fig. 2.

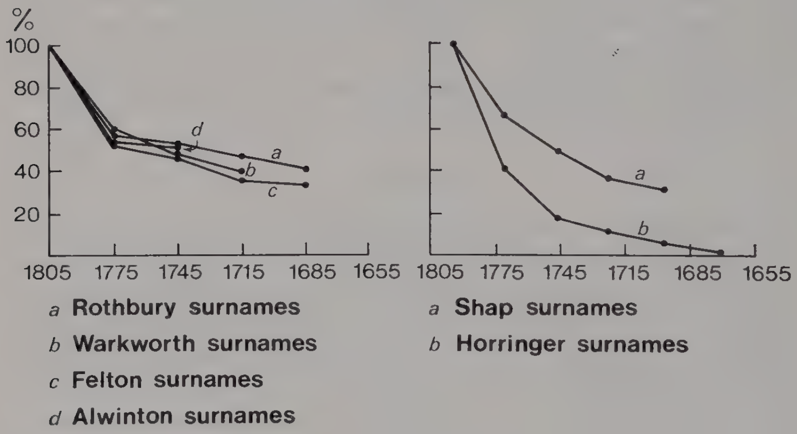

FIG. 2

Two results emerge from the comparison. First, all four parishes in Northumberland show the same level of constancy despite their completely different geographies. Secondly, when comparing the Northumbrian parishes with those of Shap in Westmorland and Horringer in Suffolk, there are marked differences. Only 2 per cent of the names remain in the earliest period in Horringer compared with about 40 per cent in Northumberland. Shap retains about 35 per cent of its names. This suggests that there is a marked difference in genetic constancy at least between Horringer and the rest, and that the Northumberland parishes show a high level of continuity.

TABLE 1. Retention of surnames

	Warkworth				Felton					Rothbury					Alwinton		
	1690 –1719	1720 –1749	1750 –1779	1780 –1809	1660 –1689	1690 –1719	1720 –1749	1750 –1779	1780 –1809	1660 –1689	1690 –1719	1720 –1749	1750 –1779	1780 –1809	1720 –1749	1750 –1779	1780 –1809
1660 –1689					**193**					**193**							
1690 –1719	**248**				101 52·6%	**192**				122 49·0%	**249**						
1720 –1749	141 52·0%	**271**			106 41·3%	126 49·0%	**257**			120 50·2%	145 60·7%	**239**			**110**		
1750 –1779	124 43·1%	116 40·3%	**288**		89 38·2%	97 41·6%	130 55·8%	**233**		104 46·2%	115 51·1%	136 60·4%	**225**		55 61·1%	**90**	
1780 –1809	113 38·6%	142 48·5%	175 59·7%	**293**	90 32·6%	97 35·1%	131 47·5%	144 52·2%	**276**	87 41·2%	100 47·4%	111 52·6%	121 57·4%	**211**	38 50·7%	40 53·3%	**75**

Despite the similarity of loss rates between the Northumberland parishes there is evidence that they contain different and partially isolated genetic populations since only a small proportion of the surnames are common to adjacent parishes. Table 2 shows the results of a comparison of surnames between parishes for the period 1720–1809. There is a clear gradient of names moving away from each parish; thus, of 498 different names found in the Warkworth baptisms in this period, only 222 also occurred in Felton, 191 in Rothbury and 93 (19 per cent) in Alwinton. Such a gradient could occur only in situations where there was restricted movement of males, and thus some restriction of gene flow between the communities.

TABLE 2. Surname gradients between parishes 1720–1809

	Alwinton	Rothbury	Felton	Warkworth
Alwinton names	165	121	104	93
Rothbury names	121	368	200	191
Felton names	104	200	451	222
Warkworth names	93	191	222	498

Marriage Distances

Another aggregative method which describes more precisely the form of gene migration is the analysis of marriage distance. In genetic terms the most important component of population movement is the net parent to offspring distance between the birth places of successive generations. This can generally be measured only on reconstructed data. However an important part of this distance is the movement of each partner for marriage, and this is especially so in a stable rural community where most of the population are tied to a locality by their work. The shortcomings of marriage distance as an estimator of parent-offspring distances are that marriage entries in the registers may give either the place of birth or the place of residence at marriage of each spouse, and that place of marriage is not necessarily the place of subsequent residence.

In Table 3 the various types of marriage in each parish are totalled for the available 50 year periods from 1811 back. Comparative data

TABLE 3. Numbers of intra- and extraparochial marriages

Parish	Period	(a) total number of marriages	(b) Male indigenous female indigenous (as % of a)	(c) Male not indigeneous female indigenous (as % of a)	(d) Male indigenous female not indigenous (as % of a)	(e) Male not indigenous female not indigenous (as % of a)	Admixture rate	Intra community (as % of b)
Warkworth	1689–1711	280	248 (88·6%)	23 (8·2%)	9 (3·2%)	0	0·057	180 (72·6%)
	1712–1761	658	510 (77·5%)	123 (18·7%)	25 (3·8%)	0	0·112	
	1762–1811	664	461 (69·4%)	170 (25·6%)	25 (3·8%)	8 (1·2%)	0·159	
Felton	1662–1711	331	260 (78·5%)	52 (15·7%)	17 (5·1%)	2 (0·6%)	0·110	
	1712–1761	557	415 (74·5%)	109 (19·6%)	32 (5·7%)	1 (0·2%)	0·128	
	1762–1812	470	321 (68·3%)	132 (28·1%)	17 (3·6%)	0	0·158	
Rothbury	1662–1711	672	572 (85·1%)	68 (10·1%)	27 (4·0%)	7 (1·0%)	0·081	351 (61·4%)
	1712–1761	754	607 (80·5%)	118 (15·6%)	26 (3·4%)	3 (0·4%)	0·099	
	1762–1811	694	522 (75·2%)	150 (21·6%)	22 (3·2%)	0	0·124	
Alwinton	1719–1761	342	239 (69·9%)	75 (21·9%)	20 (5·8%)	8 (2·3%)	0·162	
	1762–1811	398	263 (66·1%)	91 (22·9%)	44 (11·1%)	0	0·170	
Charlton	1651–1700		61%			39%		
	1701–1750		67%			33%		
	1751–1800		65%			35%		
Bickenhill	1682–1756		86%			14%		
	1758–1847		82%			18%		

are included from Charlton in Oxfordshire (Küchemann, Boyce and Harrison 1967) and Bickenhill in Warwickshire (Skip 1963). In the Northumberland parishes never less than two thirds of all marriages were contracted between couples resident within the parish. From the mid seventeenth century levels of 79–89 per cent, there is a steady fall through the eighteenth century in each parish. These results represent rather higher intra-parochial marriage frequencies than those for Charlton, but rather similar to or slightly lower than those for Bickenhill. The admixture rates are naturally low in these circumstances.

More striking evidence of a localization of marriage is provided using the detailed marriage entry before the Hardwicke Act. Here in the period ending 1711, 73 per cent and 61 per cent of intra-parish marriages in Warkworth and Rothbury respectively were actually contracted between partners resident in the same community within the parish.

Similar evidence of localization comes from those marriages where one partner was drawn from outside the parish. In these the majority of the movement proves to have occurred between adjacent parishes. For example in the Rothbury marriage entries during the eighteenth century, of the 1470 marriages recorded, 1168 (79 per cent) were between two indigenous partners, and in 172 the incoming partner was from an adjacent parish. This leaves less than 10 per cent of marriages and so less than 5 per cent of marriage partners, drawn from anywhere over a single parish width away from Rothbury. Sketchmaps showing the strength of this tendency are given by Dobson and Roberts (1971).

Neighbourhood Analysis

From the surname and marriage distance analyses, it seems reasonable to conclude that there was a high level of genetic continuity within a parish and that there would be some degree of isolation between parishes. It is really rather difficult to quantify the genetic isolation or to assess its consequences from these data. To both of these problems can be applied one of the theoretical models of population structure. Three are available, the Island, and Isolation by distance models of Sewall Wright (1969) and the Stepping Stone model of Kimura and Weiss (1964).

The isolation by distance model appears most suitable. In this, the population is considered to be continuously distributed over a wide area, with no absolute barrier to gene movement, only a decrease of movement between two points with the increase of their distance apart.

The first assumption is a reasonable approximation to population distribution in mid-Northumberland and is certainly closer than either the isolated groups of the Island model or the equally sized and spaced groups of the Stepping Stone models. Similarly, the second assumption is an approximation to reality, the frequency of marriage and so indirectly gene flow certainly decreases with distance although there are obviously effects from the occasional high density cluster of individuals in a town and from geographical and social influences.

The genetic consequences of the model depend largely upon the size of the "neighbourhood", which is the number of individuals within a section of the population which can be considered to be the equivalent of a panmictic unit in any generation. The ability to calculate neighbourhood size depends upon knowing the distances between the birth places of parents and offspring measured in one direction. This distance can usually only be obtained from parish registers after "family reconstruction" but in the north eastern registers, thanks to Bishop Barrington, it is possible to extract this distance direct from the entry in the baptism register between 1797 and 1812.

The Alwinton, Rothbury and Felton records have been used to calculate neighbourhood sizes for these three parishes. In the Warkworth records the parish of female birth is only given irregularly so that this parish has been excluded.

The axial North-South and East-West distances from the parish of birth of the parent to Alwinton, Rothbury or Felton were measured. It was necessary to assign all parents from a particular parish to the central geographical point of the parish since the records gave no details about the actual place of birth within the parish. Because of difficulty in identifying places, all parents drawn from outside Northumberland were excluded. This represented 24 (18 per cent) births in Alwinton, 95 (12 per cent) births in Felton, and 109 (9·7 per cent) in Rothbury. Because of this both mean and standard deviation will be underestimated. Parents born in either Alwinton, Rothbury or Felton are included as zeros in the appropriate cases. The results are given in Table 4. Measurements on the north/south axis are larger than those on the east/west in Rothbury and Felton, since movement in the latter is restricted to the east by the North Sea and to the west by the Cheviot Hills, but in Alwinton, movement is greater on the east-west axis since the valley of the River Coquet runs in this direction, making contact easier than over the hills in the north-south direction. In each case the distances moved by female parents are larger than those by the male which is the result of a society in which the males work and own property and so tend to be more settled than the females.

TABLE 4. Axial movement from birth of parent to birth of offspring in miles

Rothbury	East/West axis		North/South axis	
	$\bar{x}$	σ	$\bar{x}$	σ
Male parents	2·744	4·447	2·912	5·437
Female parents	4·277	4·570	5·133	7·090
Male and female parents combined	3·504	4·587	3·993	6·424

Alwinton	East/West axis		North/South axis	
	$\bar{x}$	σ	$\bar{x}$	σ
Male parents	5·560	7·792	3·042	5·566
Female parents	6·658	6·333	7·946	9·014
Male and female parents combined	6·072	7·155	5·326	7·756

Felton	East/West axis		North/South axis	
	$\bar{x}$	σ	$\bar{x}$	σ
Male parents	3·671	5·563	3·909	6·491
Female parents	4·709	7·286	5·320	7·529
Male and female parents combined	4·194	6·436	4·700	7·080

Wright (1969) defines the neighbourhood as the effective population number in a circle of radius 2σ of the parent to offspring distance in one direction. Thus the neighbourhood areas for the two parishes could be obtained from the data in Table 4. The results are presented in Table 5, column 2. The area of an ellipse was used to accommodate the unequal axial means. The effective population size within the neighbourhood was calculated in two stages. First the estimated number of parents in the area was calculated, and secondly this figure was adjusted to allow for the lessening of effective size by parents having different numbers of offspring.

Rothbury covered an area of 52·5 square miles and contained 540 parents in the period studied, while Felton covered 23·8 square miles and contained 410 parents, and Alwinton covered 64 square miles and contained 233 parents. Combining these data gave an estimate of 8·42 parents per square mile over these three parishes. Assuming this density to be typical of the neighbourhood gave estimates of the parental population of the neighbourhoods as shown in Table 5, column 3A.

TABLE 5

Source		Neighbourhood area (in sq. miles) $\pi(2\sigma_{e-w})(2\sigma_{n-s})$	Number of parents in neighbourhood		Effective size of neighbourhood	
			From area (A)	From parish (B)	From A	From B
Alwinton	Male parents	545·2	4591	2490	2774	1504
	Female parents	717·6	6042	4116	3650	2487
	Male and female parents	697·6	5874	3741	3549	2260
Rothbury	Male parents	303·9	2559	2528	1322	1306
	Female parents	407·3	3430	4283	1772	2213
	Male and female parents	370·4	3119	3132	1612	1618
Felton	Male parents	453·9	3814	6444	2422	4093
	Female parents	689·6	5806	8811	3688	5597
	Male and female parents	572·8	4823	8246	3063	5238

An alternative method of calculating the parental population involved the correction of the known total population size of each parish at the 1801 census, by the factor produced by dividing the combined number of parents in Alwinton, Felton and Rothbury by their total population in the census. (i.e. Population size of

$$\text{parish X} \times \frac{\text{No parents in Alwinton, Felton \& Rothbury}}{\text{Population size of Alwinton, Felton and Rothbury}}\Big)$$

The value of this factor is $\frac{1066}{4367} = 0{\cdot}244$

The neighbourhood parental size was then calculated as the sum of the estimated parental size of each parish, whose central point was within the neighbourhood area. Estimates by this method are given in Table 5, column 3 B. The results are similar from both methods.

The effective population size is reduced by the fact that parents leave different numbers of offspring. Two formulae are available for making the correction:

(a) $$Ne = \frac{N\bar{k}(N\bar{k}-1)}{(N-1)\sigma_k^2 + Nk(k-1)}$$

where N = the actual number of parents, $\bar{k}$ = the mean number of offspring from each parent which contributes to the subsequent generation, and σ_k^2 = the variance of the number of such offspring.

(b) $$Ne = \frac{4N-2}{\sigma_k^2 + 2}$$

in the special case where $\bar{k} = 2$ and thus population size remains constant (Li 1955).

The numbers of offspring *baptized* to each parent are available direct from the records and are given in Table 6. First are shown the numbers baptized in the period studied, which will be a considerable underestimate since many families will be incomplete, secondly the numbers estimated from details of the parity of the last child of each sex born to any parents. This will be more accurate than the first results since children born before the period will be included. However, children born after the period are still excluded and so the results are still underestimates.

TABLE 6. Family size

		Alwinton	Rothbury	Felton
Using baptisms	mean	2·22	2·11	1·93
	variance	2·91	2·24	1·83
Using parity data	mean	3·16	3·57	2·96
	variance	4·62	5·74	4·30

The fact that mean family size is considerably more than two in all parishes argues for the use of formula (a). However, the pre-marital mortality level was undoubtedly high at this time in history so that the number of offspring contributing to the next generation is likely to be lower than the number of baptisms. If all the baptized children survived and produced children at the same rate as their parents, then the population size would be expected to increase by about 50 per cent per generation. In fact between the censuses of 1801 and 1857, which represents two human generations, the populations of Alwinton, Rothbury and Felton rose by only 16, 14 and 13 per cent respectively, with no evidence of large scale emigration. Because of this population size was considered to be static and formula (b) applied.

The variance of the mean offspring number was used direct in the formula. Crow and Morton (1955) showed that the ratio of the variance to the mean of family size is a function of mean family size assuming random survival, so that with the reduced survival mean, the variance should also be reduced. This was not done for two reasons, first that the variance of baptismal mean was already an underestimate as already discussed, secondly the assumption of random mating is not likely to apply—all the offspring of a wealthy family perhaps surviving while the entire family of poorer parents perished. This would have the effect of increasing the variance.

Effective population sizes for all the estimates of parent numbers are given in Table 5 columns 4A and B. Taking into account the inexact methods involved, it seems safest to conclude that neighbourhood size in these parishes was somewhere between 1000 and 4000 at the end of the eighteenth century. This estimate is very close to that found by Alström and Lindelius (1966) in Sweden, where between 1800 and 1824 neighbourhood size ranged from 900–3000, and probably above the figure in present-day primitive communities such as the Dinka for whom an estimate of approximately 1400 was made (Roberts 1956).

Turning to the genetic consequences of the neighbourhood size (Ne_n), the most easily detectable effect is the level of genetic drift. Wright (1969) has shown that for appreciable drift to occur Ne_n should be <1000 and that it is likely to be important only when $Ne_n < 200$. From the estimates of Ne_n for these parishes it seems unlikely that drift would have played an important role in the evolution of their populations. However, these estimates of neighbourhood size apply to only a small period of time. Since population mobility showed a marked increase during the nineteenth century it is probable that neighbourhood sizes increased during this period and that in modern populations they are considerably larger than those investigated, and so the importance of drift would have been reduced even further. It is more difficult to say what earlier sizes would have been. Table 2 shows a steady increase in the admixture rate of each parish through the eighteenth century, which suggests that earlier neighbourhoods may have been smaller, but the exact relationship cannot be determined without "family reconstruction" or some alternative records giving parent-offspring distances for the earlier periods.

In concluding that drift effects are small, it is also important to remember that throughout this model the assumption of random mating is made and yet we know that man is notoriously assortative in his mating. Whether historical populations were sufficiently assortative to allow small pockets of inbreeding to occur in the general pattern of outbreeding we cannot say. Harrison *et al.* (1970a and b) demonstrated the marked assortative mating for social class on Otmoor, but concluded that contact between the classes was still sufficient for genetic homogeneity.

Conclusion and Summary

Preliminary analysis of surnames and marriage distances suggested restriction of gene flow between, and appreciable genetic continuity within, Northumberland parishes. The present analysis attempts to quantify these by applying the model of isolation by distance to the material. It appears that population size and distribution combined with the amount and distance of gene flow produced an effective neighbourhood size sufficiently high to restrict random differentiation of local gene frequencies to a relatively low level.

To discover whether these results are indeed in contrast to the impressions from the preliminary analysis and the isonymy study of Warkworth parish (reported on p. 83), or whether they represent inadequacy of the model or its application or interpretation in the present instance, calls for further investigation. At all events, the findings suggest the need for caution in accepting conclusions on population structure derived from a single method of analysis.

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A STUDY OF ISONYMY

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ISONYMY is defined as identity in surname. Crow and Mange (1965) elaborated an idea originally suggested by Muller that inbreeding coefficients could be calculated from the frequency of isonymous marriages (i.e. marriages between persons of the same surname) in populations in which pedigree or other information is either lacking or incomplete. The suggestion is based upon the constant relationship between the probability of affinal relatives having the same surname (P) and the inbreeding coefficient of their possible offspring (F) such that P/F is always equal to 4. Thus for sibs the probability of having the same surname (P) is 1 and the inbreeding coefficient (F) for offspring of a sib-marriage is $\frac{1}{4}$ so that $P/F=4$. Similarly for first cousins $P=\frac{1}{4}$ and $F=\frac{1}{16}$ and for second cousins $P=\frac{1}{16}$ and $F=\frac{1}{64}$ so that P/F is again equal to 4. Apart from exceptions that can arise from gross cumulative inbreeding or from ancestor-descendant marriages, the majority of inbreeding situations are covered by this relationship and in populations in which surnames are transmitted in a regular (usually unilineal) pattern they can be used to reflect the inbreeding coefficients of the total populations from which they are taken.

The probability of an isonymous marriage occurring at random in a randomly mating population is equal to the total of the products of the frequencies of each surname in the male and female components of the population. If "p" is the proportion of males in the population with a particular surname and "q" is the corresponding proportion of females, then the frequency of random marriage in which both partners will have that name is pq and the contribution this makes to the overall inbreeding coefficient of the population is $pq/4$. This function, summed over all surnames, thus becomes $\Sigma p_i q_i/4$. The inbreeding coefficient itself comprises 2 components. First there is inbreeding that is "circumstantial" (i.e. the chance coming together of relatives in conditions of panmixia) and second there is that which is a deliberate deviation from random mating. Random inbreeding is usually the result of consanguineous matings occurring at random in a finite population—largely as a result of the very finiteness of the population, as has been well illustrated for matings among the early population of Tristan da Cunha (Roberts 1967). It is represented by Allen (1965) as F_r and it is to this component that isonymy specifically relates. Crow and Mange (1965) show how this relationship can be used in isonymy studies to calculate both F_n, the non-random component of F, and F itself, the inbreeding coefficient of the population at large, using the following related formulae

$$F_r = \frac{\Sigma p_i q_i}{4}$$

$$F_n = (P - \Sigma p_i q_i)/4(1 - \Sigma p_i q_i)$$

where "P" represents the proportion of isonymous marriages that occur in the population

and

$$F = F_n + (1 - F_n)F_r$$

The technique was first tested by Crow and Mange on the Hutterite population. By it they showed that the average relationship in the population was of the order of something between first and half-first cousins ($F = 0 \cdot 0495$) and furthermore that almost all of this inbreeding effect could be attributed to random causes rather than to any deliberate marital policy or custom on the part of the Hutterites themselves. F_r comprised 90 per cent of the total value of F compared to only 10 per cent for F_n, which is not significantly different from zero.

Present study

The few studies of isonymy that have appeared since 1965 have tended to choose similar small, nearly closed (or actually isolated) populations (Hussels 1969, Lasker 1969, Yasuda and Furusho 1971, Lasker *et al.* 1972), which have been known beforehand to satisfy most of the assumptions of isonymy—in particular that identity of surname is a likely, if not in fact certain, reflection of common ancestry. It appeared desirable for two reasons to explore the applicability of the technique to English historical populations. First, to date there has been no investigation of inbreeding in England, and secondly it is not at all clear (Dobson and Roberts 1971) whether sufficient information will be available from parish records for the calculation of inbreeding by any of the standard methods. It was also considered a useful opportunity to assess the possibility of applying the technique to a subpopulation that is not closed but on the contrary remains open both geographically and socially to interaction with the larger mainstream population around it.

The subpopulation concerned was taken from the Anglican parish of Warkworth in Northumberland, which lies on the Northumbrian coast approximately mid-way between Holy Island and the Tyne estuary. Data on the subpopulation were taken from transcriptions of the parish marriage registers, which were found to be virtually complete for a period of 125 years, dating from 1686 to 1812. Over 1600 entries provided the names of all the marriage partners for the period together with their place (or parish) of residence. Variations in the spelling of names were numerous and place- and parish-names in particular were not immune from gross distortion, often along the lines of regional accent or dialect, having obviously been spelt as they were pronounced locally. The parish of "Shilbottle" for example became anything from "Shivilbittle" to "Shell Bettel", "Berling" curiously became "Berlin", and, although most variations like this are not difficult to identify, unfamiliarity with an area may lead to considerable confusion. Variations in the spelling of surnames were also common and, although these were corrected using the outline for historical populations suggested in Steel (1968), some problems still remained as to the interpretation of certain possibly isonymous unions. The marriages of Thomas Boudon and Barbara Bouton both of Warkworth and of Johannes Willson and Anna Wilson for instance may or may not be isonymous. According to Steel, "Boudon" becomes "Bowden" and "Bouton" becomes "Bolton", changes that are in fact more extreme than if the surnames were considered the same in the first place. Similarly one has to consider whether "Willson" is likely to be a mis-spelling for "Wilson" or whether in view of the fact that the marriage partners both come from the same location the two are actually quite deliberately differentiated. In this study the Boudon-Bouton marriage was not taken to be isonymous but the Willson-Wilson marriage was. Uncertainties of this type are important to consider since, though not doing so in the present study, they could seriously affect the results of any isonymy survey by their effect on the proportion of isonymous marriages in the populations.

Results

The registers were arbitrarily divided into 5 consecutive periods of 25 years—1686 to 1711, 1712 to 1736, 1737 to 1761, 1762 to 1786 and 1787 to 1812—and were dealt with in 5 different ways. First the number of marriages was counted for each period together with the number of different surnames used and the number of surnames that were used only once—these "unique" names obviously precluding the possibility of isonymy since the appearance of the name in one sex was not complemented by its appearance in the other. These results are set out in Table 1,

TABLE 1. Number of marriages and surnames analysed from Warkworth Marriage Registers 1686–1812

	1686–1711	1712–1736	1737–1761	1762–1786	1787–1812
No of marriages (n)	279	327	332	381	277
Total no. of surnames used	558	654	664	762	554
No. of different surnames used	239	248	256	308	252
No. used only once ("unique")	155	164	156	213	174
Proportion unique	0·65	0·66	0·61	0·69	0·69

All unions included. The registers were then taken as a whole without parish origins being taken into account so that both inter- and intra-parish unions are included. For each 25 year period the following were calculated (i) the total number and proportion of isonymous marriages (ii) the random expectation of isonymy and (iii) respective values of F, F_r and F_n. These produced the results set out in Table 2. This shows an increasing number of isonymous marriages occurring over time and a corresponding increase in the value of F, of whose total F_n—the non-random inbreeding component—takes an ever increasing proportion rising from 8 per cent in the first 25 years (1686–1711) to 82 per cent of the inbreeding total in the last period (1787–1812). The negative value of F_n in the second quarter-century is probably due to chance, though negative values of non-random inbreeding can imply a positive avoidance of consanguineous marriages in a population. At what level such values become significant however is not yet clear.

TABLE 2. Analysis incorporating all unions

	1686–1711	1712–1736	1737–1761	1762–1786	1787–1812
No. of isonymous marriages	2	2	4	6	8
Proportion of total number of marriages (P)	0·0072	0·0061	0·0120	0·0157	0·0288
Total random expectation	1·842	2·361	2·217	2·034	1·480
Random expectation $\left(\Sigma p_i q_i \text{ or } \frac{TRE}{n}\right)$	0·0066	0·0072	0·0066	0·0053	0·0053
(F_r) $\left(\frac{\Sigma p_i q_i}{4}\right)$	0·00165	0·0018	0·00165	0·0013	0·0013
(F_n) $(P-\Sigma p_i q_i)/4(1-\Sigma p_i q_i)$	0·00015	−0·00028	0·00135	0·00261	0·00590
(F) $(F_n+[1-F_n]F_r)$	0·0018	0·00152	0·00299	0·00391	0·00719

Intra-parish unions only. The same set of calculations was made again on the registers, but this time inter-parish unions were excluded. The results are shown in Table 3. As can be seen there are changes in the number of isonymous marriages and in the levels of random expectation but the overall trend is the same (Fig. 1), that the number of isonymous marriages and the corresponding values of F and F_n all increase over time (in this case F by a factor of 4 and F_n by a factor of 15).

TABLE 3. Analysis with only intra-parish unions included

	1686–1711	1712–1736	1737–1761	1762–1786	1787–1812
No. of isonymous marriages	2	2	2	4	8
Proportion of total no. of marriages (P)	0·0072	0·0061	0·0060	0·0105	0·0288
Total random expectation	1·573	1·933	1·666	1·543	1·054
Random expectation ($\Sigma p_i q_i$)	0·0056	0·0031	0·0050	0·0040	0·0038
(F_r)	0·0014	0·00078	0·00125	0·0010	0·00095
(F_n)	0·0004	0·00075	0·00025	0·00163	0·00627
(F)	0·0018	0·00153	0·0015	0·00263	0·00721

However in neither case could these analyses guarantee the assumption that isonymy was a reflection of genetic relationship. Even isonymous intra-parish marriages are not proof of this since in Northumberland rural parishes tend to be quite large in area and Warkworth is no exception, covering roughly 28 square miles. This is certainly extensive enough to suggest that someone with a particular surname in the extreme north of the parish is not necessarily related to someone with the same surname living in the parish's extreme south. It is also the case when such distances are involved that someone, who lives near the parish boundary, will in fact be closer geographically to villages and hamlets in neighbouring parishes than to others in his own—an important factor that was excluded in the second analysis and included only in part in the first.

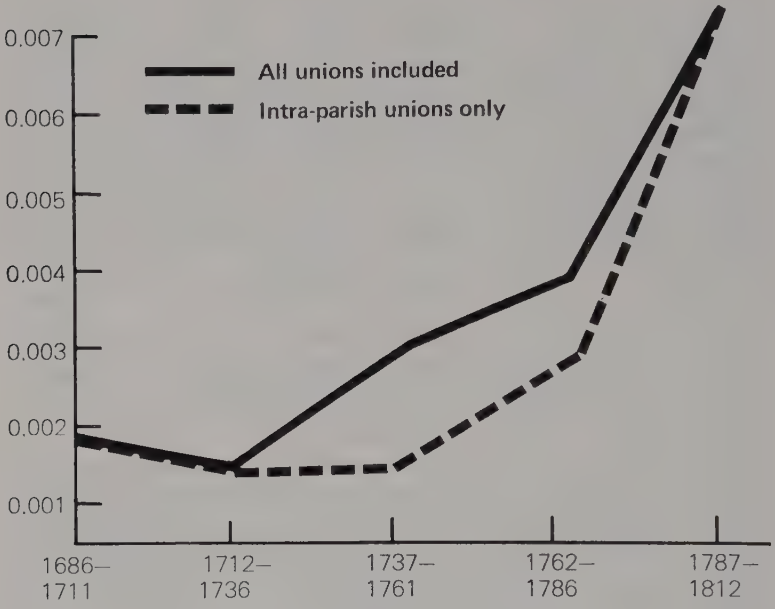

FIG. 1

Geographical distance. For this reason three further analyses were made that disregarded parish boundaries and were based instead purely on geographical distance, taking as reference points distances of 10 and 20 miles and, where it was possible, of 5 miles as well to represent limits beyond which relationship between isonymous pairs could not be assumed. Geographical distance is admittedly neither the safest nor the most refined method of basing likelihood of relationship, but previous work on the Northumberland area (Dobson and Roberts 1971) has suggested that there was a high degree of population constancy and localization in Northumberland during the eighteenth century and thus it appears likely that closeness of family ties will be reflected in geographical distance from the place of residence of marriage partners.

First the number of isonymous marriages, their proportion in the population and the random expectation of isonymy were calculated for marriages contracted within a 10-mile radius of the actual village of Warkworth, and secondly for those contracted within a radius of 20 miles. The results of these calculations are set out in Tables 4 and 5. They reflect quite clearly the same trends that were found before—of isonymy increasing eventually 3-fold within the same number (n) of marriages, of the multiple increase in F_n, and of F increasing from a very low 0·0018 to a level that, like all the results for the last quarter-century, reflects an average degree of relationship between marriage partners in the area of something just greater than fourth cousins.

TABLE 4. Analysis of unions contracted within a 10-mile radius of Warkworth village

	1686–1711	1712–1736	1737–1761	1762–1786	1787–1812
No. of isonymous marriages	2	2	3	5	7
Proportion of total no. of marriages (P)	0·0072	0·0061	0·0090	0·0131	0·0253
Total random expectation	1·703	2·1804	1·9157	1·7323	1·2527
Random expectation ($\Sigma p_i q_i$)	0·0061	0·0066	0·0058	0·0045	0·0045
(F_r)	0·00152	0·00165	0·00145	0·00112	0·00112
(F_n)	0·00027	−0·00012	0·0008	0·00215	0·00522
(F)	0·0018	0·00153	0·00225	0·00327	0·00633

Study of marriages contracted within a 5-mile radius was hampered by the fact that from 1737–1812 a large number of entries in the parish registers recorded only the parish of origin of each marriage partner and not a more specific village or hamlet place-name.

TABLE 5. Unions contracted within a 20-mile radius of Warkworth village

	1686–1711	1712–1736	1737–1761	1762–1786	1787–1812
No. of isonymous marriages	2	2	4	6	8
Proportion of total no. of marriages (P)	0·0072	0·0061	0·0120	0·0157	0·0288
Total random expectation	1·803	2·2752	2·0301	1·9396	1·3755
Random expectation ($\Sigma p_i q_i$)	0·0065	0·0070	0·0061	0·0051	0·0050
(F_r)	0·00162	0·00175	0·00152	0·00127	0·00125
(F_n)	0·00017	−0·00022	0·00148	0·00266	0·00597
(F)	0·0018	0·00153	0·0030	0·00393	0·00721

However study was possible in the first 3 quarter-centuries and calculations were made as before but in this case using as reference a radius of 5 miles from the place of origin of one or other marriage partner and not arbitrarily from Warkworth village. The results (Table 6) show the beginning of the same trends as were found before and that have been consistent with all the levels of refinement of analysis it was thought possible to use.

TABLE 6. Unions contracted within a 5-mile radius of home of one or other marriage partner

	1686–1711	1712–1736	1737–1761
No. of isonymous marriages	2	2	2
Proportion of total no. of marriages (P)	0·0072	0·0061	0·0090
Total random expectation	1·620	2·131	1·470
Random expectation ($\Sigma p_i q_i$)	0·0058	0·0065	0·0044
(F_r)	0·00145	0·00162	0·0011
(F_n)	0·00035	−0·0001	0·00115
(F)	0·0018	0·00152	0·00225

Discussion and Conclusion

One question raised by these results concerns the significance of this consistent trend. In all cases the value of F rises to a level that is much higher than that calculated by more conventional methods for any other European peasant community. Some examples of these values for comparable periods are set out below:

Place	Date	Method	*F*	
Warkworth	1787–1812	isonymy	0·0063–0·0072	
N. Italy	1787–1812	dispensation	0·000325	(Moroni 1967)
Sardinia	1800–1849	dispensation	0·00058	(Moroni 1966)
France	1812–1954	dispensation	0·0011	(Sutter and Tabah 1955)

The Warkworth figure also rises to more than twice that estimated by Moroni (1967) for the isolated Aeolian Islands for the period 1825–1844 ($F=0\cdot0033$) and compares with the following estimates made for other isolated communities at later periods:

Place	Date	Method	*F*	
Warkworth	1787–1812	isonymy	0·0063–0·0072	
Ramah Navaho	1820–1948	pedigree	0·0066	(Spuhler and Kluckhohn, 1953)
Protestant Rhine isolate	1840–1889	pedigree	0·0050	(Nollenburg 1932)
Hutterites	1874–1960	pedigree	0·0216	(Mange 1964)
Hutterites	1874–1960	isonymy	0·0495	(Crow and Mange 1965)
Hohenzollern Jews	1875–1920	pedigree	0·0110	(Reutlinger 1922)

The overall suggestion is quite clearly of an inbreeding level more akin to that estimated for isolates by pedigree analysis than that for open populations estimated from the methodologically more similar analysis of the frequency of dispensations for cousin marriage. This is consistent with the suggestion that there was a high degree of population constancy and localization in Northumberland in the eighteenth century. However it seems that migration actually increased during that century (Dobson and Roberts 1971) and that the degree of population constancy and localization thus *declined* over time (in contradiction to the inbreeding values). It seems from this information that the high F value must represent an overestimation of the true figure, a bias deriving in part from the continual loss of certain names from the mating population and in part from errors made in the basic assumption upon which isonymy is based. Exactly how great this overestimation may be is not clear.

If we take as an upper limit the increase in the level of migration, 21·6 per cent, a correction by a similar factor of the value of F would still produce a high result of 0·00564 which, even though inflated by the other factors that may make isonymy overestimate actual inbreeding, still suggests a rather closed, locally mating population, that may well have evolved somewhat independently of other surrounding similar entities or may largely have retained its original distinctive genetic constitution. There is no way of telling how great any further included exaggeration may be. Only when the one population has been subjected to both an isonymy study and a full pedigree analysis will it be possible to show by how much isonymy does overestimate inbreeding.

Isonymy then has provided some indication of the level of inbreeding for a population and for a period for which other methods of analysis, in the absence of specific pedigree data, seem impossible. The usefulness of isonymy has been claimed before—its theory is reasonably straightforward, the technique itself is relatively simple to apply. In Crow and Mange's original study isonymy proved its worth by revealing a hidden store of inbreeding that doubled original estimates for the Hutterite population. It is the conclusion of this paper that, as long as its results are treated with the caution indicated, isonymy can be equally applicable and useful in providing estimates of inbreeding from historical data and from the records of non-isolated populations, thus yielding positive evidence about populations and situations in time concerning which we have previously only been able to speculate.

Acknowledgements

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THE STRUCTURE OF POPULATIONS LIVING ON HOLY ISLAND, NORTHUMBERLAND

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HOLY ISLAND is a small L-shaped piece of land lying just off the coast of rural Northumberland some 10 miles south of Berwick on Tweed. It is joined to the mainland twice a day at low water and so experiences a semi-isolation which has remained unchanged for many centuries.

About 175 people live in the village on Holy Island and most of them have been examined for a wide range of population variables. This sample of living islanders is genetically unique. Out of 25 unifactorial genetic systems, 14 have statistically significant differences when compared with samples from the Northumbrian mainland, 2 more are just not significant at the 5 per cent level of probability and comparisons are impossible for 5 other traits due to the absence of genotypic variation. The sample is also apparently different in its dermatoglyphic results and other variables such as differential finger length, joint sense and tongue rolling.

It is difficult to enumerate the inhabitants exactly because of a continual but small population movement. However it is possible to subdivide the living group into three genetically meaningful categories;

Group (a). Those with a large number of kin ties on the island, who were born on the island, who have a characteristic island surname, and who have lived most of their lives on the island. On average one person from this group is related to 78 others. There are about 100 individuals in this category.

Group (b). This is the subgroup who marry islanders and who live on the island but who were born elsewhere. This group usually, but

FIG. 1. Example of a cohort work sheet (No. 21) Unrevised

		Cohort 1770–79									Number 21							
Name father	Name mother	Offspring									Birth-Interval							
		1	2	3	4	5	6	7	8	9	–2	–3	–4	–5	–6	–7	–8	–9
*Allen Thos.	*Wilson Raechel	M	M +	F	F	M +	F +	M			30	28	31	29	30	31		
*Allison Geo.	*Grey Raechel	M	F	M +	F +	M +	F				26	36	37	30	31			
Angus Jas.		F																
Bateson Rbt.		M																
Brown Thos.	Sibbit Mary	M	M	M	M						23	49	38					
Burn Jos.		M	M	M +	M	F					27	34	21	33				
Cobb Jos.	*Reavley Mary	M																
Grant Jas.		M																
*Grey Geo.	*Watson Jane	F	M +	F	F +	M	M +	M	M +		13	18	37	34	38	34	49	
*Grey John		M +																
*Jackson Will.	*Wilson Dorothy	M +	M +								24							
*Lilburn Rbt.	*Taylor Eliz.	M	M	M +	F	F +	F	M +	F	F +	13	27	30	36	32	51	40	16
*Lilburn Jas.	*Walker El	F																
Lisle Ralph		F																

FIG. 1. (*continued*)

		Cohort 1770–79									Number 21							
		Offspring									Birth Interval							
Name father	Name mother	1	2	3	4	5	6	7	8	9	–2	–3	–4	–5	–6	–7	–8	–9
Mather And.	Redpath Mgt.	F	M	F	F+	M					24	25	39	40				
Mather John		F	M								16							
Moffett Rbt.		M																
*Morton Will.		M	F+	M	M						22	25	52					
Purvis And.	Reavley Phillis	M+	M	F							22	27						
Simpson John	Elliott Marjory	F	F	F	M	F	M	F			23	33	20	19	24	28		
*Watson Jas.	Burnett Jane	M	F	F							49	56						
White Will.	*Allen Mgt.	F	F	M							34	26						
*Wilson Jas.	Gibson Eliz.	M+	M	M+	M	M	F	M+	F	F+	26	26	31	11	29	43	36	57
Wilson Thos.	*Patterson Isab.	M	M+	F	M	M+	M				37	30	42	43	32			

*Birth mentioned in previous cohorts
+A parent in later cohorts.

The effective cohort for this decade includes only those parents who have one or more offspring marked with a cross.

not exclusively consists of women. There are about 25 individuals in this group.

Group (c). Those with no specific ties to the island, consisting of retired people and those who live on the island because of their trade or profession. There are about 50 individuals in this group.

When the simple genetic results are examined using these subdivisions some of the anomalies may be accounted for by an unusual sampling effect in groups (b) or (c). However other problems are also brought to light; for example, the ABO results for the whole island do not differ very much from the controls with 25 per cent A_1 and 10 per cent A_2. However when group (a) is extracted from this total it shows 14 per cent A_1 and 11 per cent A_2 whilst group (b) has 50 per cent A_1 and no A_2, and normalizes the total results. Thus a recent inflow of A_1 genes is responsible for the unremarkable total island sample.

For a better understanding of the present genetic structure of the island it is necessary to study the historical development of the community. A major component of this historical demographic study has been directed towards the fertile population. This has most relevance genetically when considering the living descendants of these past populations. Again the information about this may be extracted from the parish baptismal registers which are more complete than the marriage registers. Moreover the data from the marriage registers can be easily misinterpreted. The baptismal entries were extracted from 1578 to the present day and these results were placed into nuclear families; the fathers' names nearly always being present in the baptismal registers whilst maternal names were found through the marriage registers and other sources.

These families were then placed with others into groups whose first child was born between certain fixed periods. The first of these groups includes offspring who were born in 1578 or 1579. Thereafter the groups followed decades, 1580–89 and so on until 1960–69. This gives 40 consecutive groups or cohorts. An example of a small cohort, 1770–79 (number 21) is shown in Figure 1.

An examination of the completed results showed that the registers were in fact recording two interlocking populations. This is reflected in each of the cohorts. One of the populations has a larger number of children and often the marriage partner is known. The surnames are usually familiar and one parent at least was born on the Island and is thus recorded in earlier cohorts whilst the offspring themselves tend to become Island parents and are recorded in later cohorts. The second group is directly contrasted to this and seems to reflect fragmented sibships. The mother is usually not known, the parents were not born on the Island and also the offspring do not become parents in later cohorts. If they do re-appear in later cohorts it is only for one or two generations. The surnames are unfamiliar and there are no traceable connections with other families living on the Island. The groups are also divided professionally in that the former are often farmers, fishermen or landowners whilst the latter tend to be labourers, tradesmen or soldiers. These two contrasted populations represent on the one hand the stable and settled community and on the other the itinerant and poorer groups. The two are not entirely separate and often the one provides marriage partners for the other.

The inflow of entirely new couples into the stable segment of the population through the marriages of their offspring gives an indication of this interchange. New couples are those who produce offspring on the Island but who originated elsewhere. The children and grandchildren of these new couples are absorbed into the stable population. Many new couples are found in the earlier cohorts because of the increasing comprehensiveness of the population registration procedures in the early seventeenth century. After this time there is a general decline in the appearance of these couples who often introduce new surnames into the Island community. The unstable segment of the population, however, has a constantly high proportion of new couples entering it. The two populations are contrasted in Figure (2).

At this stage it seemed likely that the stable population was equivalent to group (a), that is the long standing Islanders in the living population, whilst the itinerant segment is probably equivalent to group (c) and group (b) being extracted from the non-islanders of group (c) or from elsewhere. Because of the dynamic nature of the two segments it is impossible to segregate the populations. It is possible to form two genetically useful subdivisions, however, which broadly correspond to these groups. This is done by extracting those individuals whose descendants in turn produce offspring on the Island in at least one further cohort. These have been called the genetically "effective population" whilst the remainder is the "non-effective population". The effective population represents the core population on the Island at any one time. This is modified each generation by new couples or new individuals married to Islanders donating offspring into this group and also by others leaving it.

This effective population may be represented as being the direct descendants of 96 new couples who contributed offspring into the group between the 1st and the 36th cohort. The majority had entered the effective population by the 20th cohort. Not all these couples contributed to the living population. In fact only 45 per cent of the new couples could contribute any genetic material to the present day Island group. The genetic endowment of these ancestors is likely to be diverse. Also the relative contribution of each ancestral couple varies widely from one cohort to the next and so it seems doubly probable that the genetic endowment of the living population would be unique. Most of the couples who contributed to the living population do so through a few common ancestors. Certain new couples are the direct ancestors of over 60 per cent of the offspring in some later cohorts. This is seen in diagrammatic form in Fig. 3 which shows the offspring of three such couples. The probability of any allele being in greater or lesser proportion in different generations depends on the contribution of the founder couples at any one time. Some of the genetic differences in the living population could be accounted for by such large variation in genetic contributions for each cohort (Fig. 3).

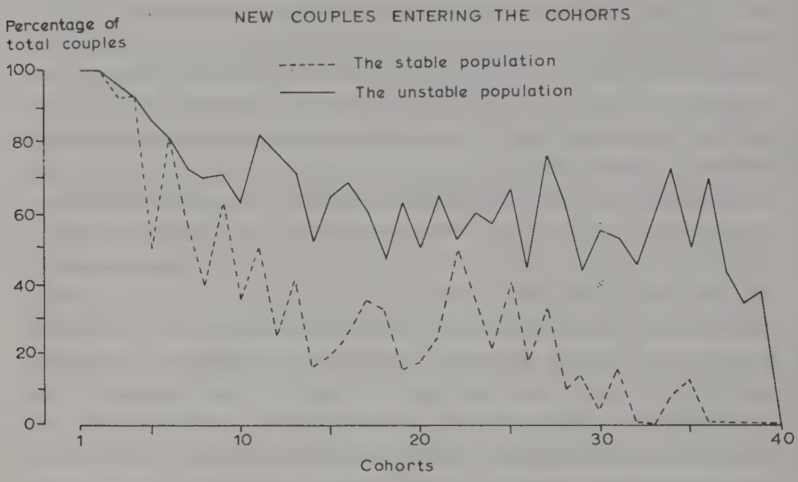

FIG. 2

The effective and non-effective populations may be contrasted by several demographic criteria. The family sizes, for examples, as recorded from the registers varies with the effective and non-effective cohorts. This is shown in Table 1, with half the number of fertile couples in the effective group producing more offspring, proportionally, than the larger number of couples in the non-effective groups.

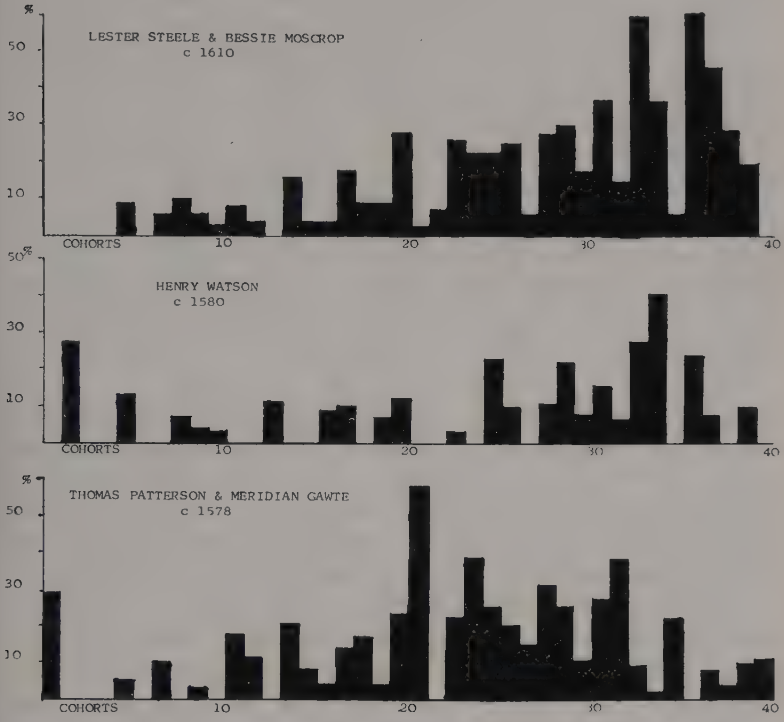

FIG. 3. The descendants of new couples. The percentage of offspring in later cohorts that are the direct descendants of named couples. (The percentages are the proportion of the total number of offspring belonging to a specific cohort).

The two contrastable populations, effective and non-effective, in terms of the living population may be comparable with groups (a) and (c). Group (b) is as important, however, in understanding the genetic heterogeneity of the island population. This group is the non-island population who marry islanders and in recent years represents the major source of gene flow into the community on the Island. The proportion of such marriages would indicate the extent of the genetic isolation of the population. The origin of the marriage partner could also be of use in estimating the possible diversity of the new genes.

TABLE 1. Family size

	Effective population			Non-effective population		
Cohorts	Number of parental pairs	Total no. of children	No. of children per couple	Number of parental pairs	Total no. of children	No. of children per couple
1–5	55	188	3·4	145	265	1·8
6–10	99	455	4·6	217	471	2·2
11–15	111	504	4·5	192	468	2·4
16–20	74	367	5·0	191	406	2·1
21–25	67	330	4·9	118	228	1·9
26–30	77	421	5·5	188	262	1·9
31–35	43	183	4·3	112	247	2·2
36–40	11	37	3·4	59	91	1·5
Totals	537	2485	4·6	1232	3538	2·1

Marriage distance is taken as the distance between birthplaces of spouses. In this instance it is considered in relation to exogamous marriages; that is one partner born on Holy Island and one born elsewhere, endogamous marriages being those between two people born on Holy Island. Marriage distance and marriage type are examined here mainly in relation to the nineteenth century. This is partly because the nature of the registers make it difficult to obtain results before this time and partly due to the fact that new couples entering the Island community petered out by the nineteenth century. There are in fact three separate sources which give these data. These are the parochial marriage registers, the baptismal entries formed into cohorts, and the enumerators returns for the 1851, 61 and 71 censuses. The marriage books omit free church and Roman Catholic marriages. Again they take no account of subsequent fertility or lack of it. The cohorts from 1790 to 1820 include nearly all the marriage partners' maiden names and places of birth; this is a feature of Durham diocese books at about this time. They are useful for providing information on the fertile segment of the community but no comparable information on the infertile marriages is available. The series of three census returns provides overlapping data at fixed periods of time rather than for specific couples, as do the cohorts. The censuses also provide data on infertile couples and have the advantage of recording only those living in the community rather than those who chose to have their baptisms or marriages recorded, whether they live on the Island or not.

Marriage distance may be used as an indicator of gene flow. However it takes no account, as defined, of the movement of individuals after birth, which could be considerable and indicate a great deal about the construction of the community. Holy Island, for example, is characterized by a high rate of migration in and out of the community; peripatetic tradesmen and labourers, soldiers and so on. The marriage distances are large but this is not necessarily due to movement of a segment of the Island population looking elsewhere for marriage partners; often it is the marriage partners who came to the Island. The results from all sources for marriage distances are compared in Table 2 and Fig. 4. The marriage distance is measured from the nearest point on the mainland: 3 miles from the village on Holy Island.

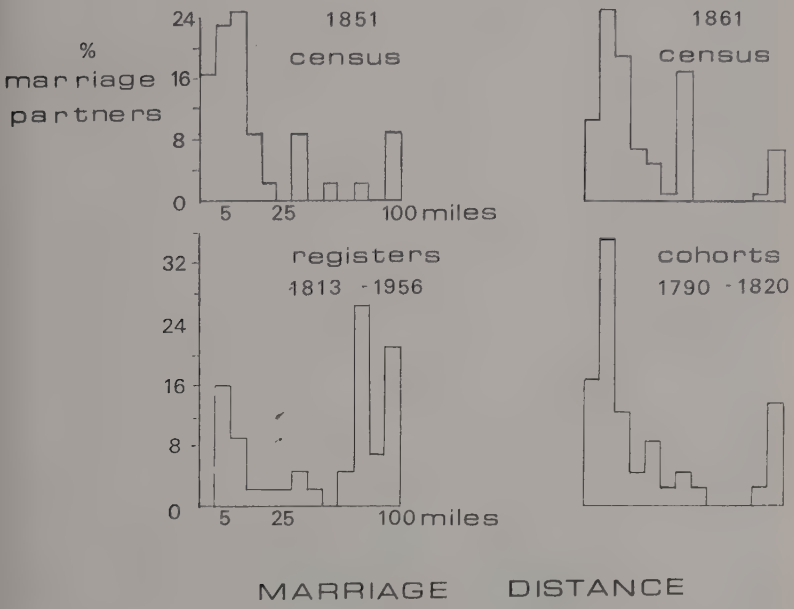

FIG. 4

TABLE 2. Marriage distances on Holy Island

	Marriage registers 1813–1958 1804–1822 (S)*				Total cohort decades from 1790–1820				1851 Census				1861 Census			
Couples	M	F	Total	% Total	M	F	Total	% Total	M	F	Total	% Total	M	F	Total	% Total
Both from Holy Island			91				33				37				29	
Neither from Holy Island			1				38				23				23	
One parent from Holy Island the other from elsewhere	38	4	42		13	35	48		12	31	43		16	36	52	
0–4 miles				0	4	4	8	16·7	2	5	7	16·3	2	4	6	11·5
5–9 miles	6	1	7	16·7	1	16	17	35·4	2	8	10	23·3	2	11	13	25·0
10–14 miles	3	1	4	9·5	1	5	6	12·5	3	8	11	25·6	3	7	10	19·2
15–19 miles	1		1	2·4		2	2	4·2	1	3	4	9·3	2	2	4	7·7
20–24 miles	1		1	2·4	2	2	4	8·3	1		1	2·3	1	2	3	5·8
25–29 miles	1		1	2·4	1		1	2·1				0		1	1	1·9
30–34 miles	1	1	2	4·8		2	2	4·2	2	2	4	9·3	5	5	10	19·2
35–39 miles	1		1	2·4		1	1	2·1				0				0
40–44 miles				0				0		1	1	2·3				0
45–49 miles	2		2	4·8				0				0				0
50–54 miles	10	1	11	26·2				0		1	1	2·3		1	1	1·9
55–59 miles	3		3	7·1	1		1	2·1				0				0
100+ miles	9		9	21·4	3	3	6	12·5	1	3	4	9·3	1	3	4	7·7
Mean distance miles	49·6	24·8	47·3		35·2	19·2	23·5		20·8	21·6	21·4		21·2	21·7	21·6	

*Scottish marriages.

The pattern of distribution is similar for the census material and for the cohort results, whilst the marriage register data is essentially different with, in this case, over half the marriages having distances of more than 40 miles with a mean of 47·3 miles. The mean for the cohort data is 20·8 mile and for the censuses of 1851 and 1861 21·4 miles. The marriage registers yield significantly different results compared with the other sources.

Marriage types are recorded, using the same sources as the marriage distances, in Table 3. The results from the census material are fairly uniform with about 34 per cent endogamy and 45 per cent exogamy. The remainder are those couples not born on the Island and these are the new couples and in this case belong to the non-effective populations. The cohorts for 1790–1820 show a similar pattern to the census results but with fewer endogamous couples. This difference may be due to non-fertile unions which are recorded in the census but not in the cohorts. It is also likely to be a reflection of an inflow of new couples attracted to the Island by the boom in herring fishing at that time. However the results from the marriage registers are again very different from the other sources with twice as many endogamous marriages as exogamous rather than fewer as in the other data. It is difficult to know how to interpret this: it is possible that large numbers of endogamous couples leave the Island, or that many exogamous marriages take place elsewhere and the couples then return to the Island. Moreover the proportions would be diluted by new couples entering the Island community. If this is so then it must be fortuitous that the proportion of exogamous marriages in the registers is similar to the proportions from other sources. There seems to be little change in the degree of endogamy in the nineteenth century on Holy Island, the cohort data and the census material being in essence similar. The decrease in outside couples in the 1871 census is a reflection of an economic and population decline which has continued almost to the present day (Table 3).

Hence it seems that for the Holy Island population 40 per cent of the couples had one partner in the community who was introducing new genetic material to the Island from an average of 30 miles away. This inflow although small in absolute numbers seems to have been constant not only for the nineteenth century but also for the three earlier centuries as well. The rate of fertile endogamy can also profoundly alter the genetic constitution of subsequent generations, by chance, in conjunction with the facts known about the ancestral

TABLE 3. Intra and extra parochial marriages—the results from different sources

Marriage partner origins	Living couples from census data 1851		1861		1871		All marriages from registers 1813–1960		All reproducing couples—cohorts 1790–1820	
	Number	%	Number	%	Number	%	Number	%	Number	%
Both born on Holy Island	32	35·6	29	29·9	34	37·8	86	66·7	33	27·5
One born on Holy Island	35	38·9	45	46·4	41	45·6	42	32·6	49	40·8
Neither born on Holy Island	23	25·6	23	23·7	15	16·7	1	0·7	38	31·7
Total	90		97		90		129		120	

contribution into later cohorts. Of the 96 couples who are potential ancestors fortuitous endogamous marriages will considerably reduce the actual minimum number of common ancestors. This has not been computed for different cohorts but the living population may be accounted for by a maximum of 7 such ancestral couples. The probability of genetic diversity for earlier generations with different sets of common ancestors is high. Also the fewer the common ancestors, the fewer the exogamous marriages and the greater the number of offspring of endogamous marriages and then the more chance effects would be expected in different generations. The number of exogamous marriages involved in the production of the living population amounts to less than 30 from the seven common ancestors.

For the living group, endogamy at a rate of about 35–40 per cent still produces a marked effect on the genetic structure of the population by inducing a "bottleneck" effect within the communities. That is, chance endogamy produces fewer genetic variables by reducing the number of common ancestors and increasing the degree of relatedness on the Island. The differential fertility of endogamous versus exogamous marriages has not been computed for the whole time span but is available for the cohorts 1790–1820. In fact for this period internal marriages produced 4·8 offspring whilst exogamous marriages give a mean of 4·4 children and so would tend slowly to increase genetic differences.

A further type of "bottleneck" situation is found on the Island. There have been two major population declines which have had the effect of restricting the gene pool considerably and for a time the mortality rate has grossly exceeded the birth rate. This tendency has been exaggerated by the differential emigration of younger people. These two periods can be found by studying the numbers of baptismal entries. The first occurred in the late eighteenth century, the decline starting in the early eighteenth century. The other has just finished having started about 1870. Both events again limit the subsequent genetic material available on the Island.

In summary, a small living community has been studied and its demographic history investigated. A variety of instances are catalogued all of which, by chance, could cause wide fluctuations of genetic polymorphisms. The degree of fluctuation would not be constant through time due to the nature of the Island population; rather each generation would differ from the last. The findings in the present population on the Island tend to confirm this hypothesis.

DEMOGRAPHIC AND GENETIC STUDIES IN THE ORKNEY ISLANDS

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A population survey of the Orkney Islands was started in 1970 with two main aims. The first is to investigate the relationship between demographic factors, including population sizes and movement patterns, and degrees of genetic heterogeneity between the Island communities. The second aim is to examine the overall affinities of the Orcadians with more southern British groups and with Scandinavian communities. In this paper, the history and population structure of the islands is discussed and the methodology of the survey considered. Preliminary results of studies on local groups and on schoolchildren are presented.

The Orkney Islands

The history of the inhabitants can be divided into three main phases (see Wainwright, 1962). The first phase, of pre-Norse populations, dates from Neolithic times. The early settlers probably reached Orkney about four thousand years ago, and were followed by Bronze and Early Iron Age peoples. Between the first and sixth centuries A.D., the communities were culturally "Broch Builders" and then "Picts". Over one hundred brochs are known at present; as each suggests a local community of between thirty and fifty individuals, the total number of inhabitants at this time may well have been several thousand.

In the second phase, after Viking colonization, the islands were annexed to Norway in the latter part of the ninth century. Many

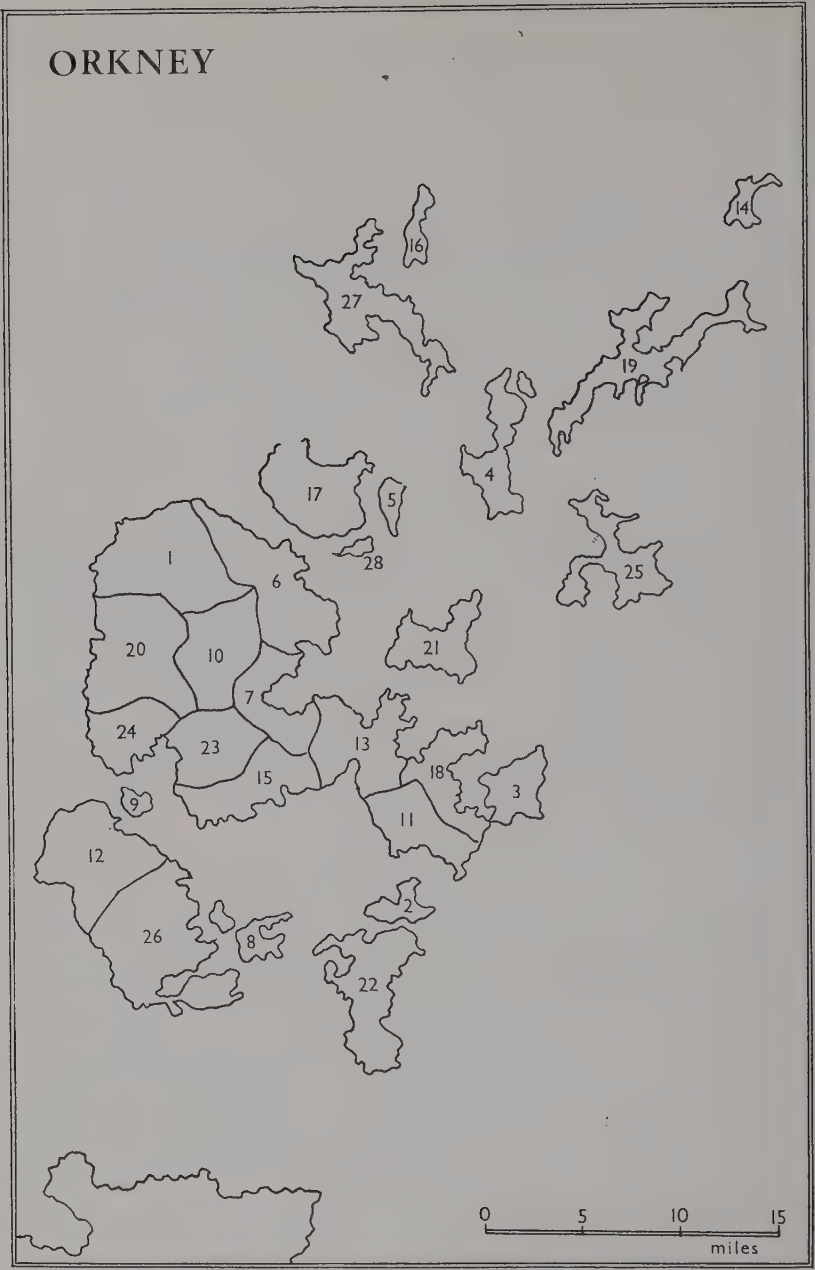

FIG. 1. The Orkney Islands. The numbers identify the 28 parishes into which the island population is divided.

present day place and farm names (the majority on many islands) have clear origins in Norse words, and were obviously in existence by at least late Norse times. This, and the fact that there are few pre-Norse names, suggests widespread Norse settlement and replacement of Pict communities.

The third phase began when, in 1468, the islands were attached to Scotland as a pledge (which has never been redeemed) for the dowry of the Princess of Denmark on her marriage to James III. This was followed by settlement of Scots from both highland and lowland areas of Scotland, a settlement which reached a peak in the seventeenth century. The extent of Scots intrusion and survival, like that of the earlier Norse settlements, can be estimated through the study of names including, for these more recent colonizations, surnames. In a study of nine cemeteries, from the northern islands and from the central Mainland island, the surnames of over five thousand individuals were examined. The three commonest surnames in each cemetery were considered and, of the 23 different surnames found, 14 were of Norse origin and 9 were of more recent date, indicating intrusive family movement from the South.

The present county of Orkney consists of a group of about seventy islands off the north-east tip of Scotland, separated from the mainland by the Pentland Firth, which although only 6½ miles across at the narrowest is a formidable barrier even today. The total area of the county is 376 square miles. There are at present just over 17,000 inhabitants, living on 25 of the islands, of which the largest is "Mainland", some 207 square miles in area.

Figure 1 shows the geographical location and arrangement of the islands and the 28 parishes into which the island population is divided. There is considerable variation in the numbers of inhabitants in the different parishes and in the changes in population size which have recently taken place (Figs. 2 and 3). Within parishes, with the exception of Kirkwall (No. 13 on Figs. 1 to 3) and Stromness (24), the inhabitants are quite evenly distributed, with little clustering into villages. The distribution of houses on the island of Sanday (19) provides a good illustration of the nature of spatial organization of the inhabitants (Fig. 4). Historical evidence (Barclay, 1965) suggests that the overall population of the county reached a peak in 1861. Since then there has been a continuous, though recently slackening, fall (Fig. 5). The fact that the population can be broken up into a number of small communities, varying in size and in

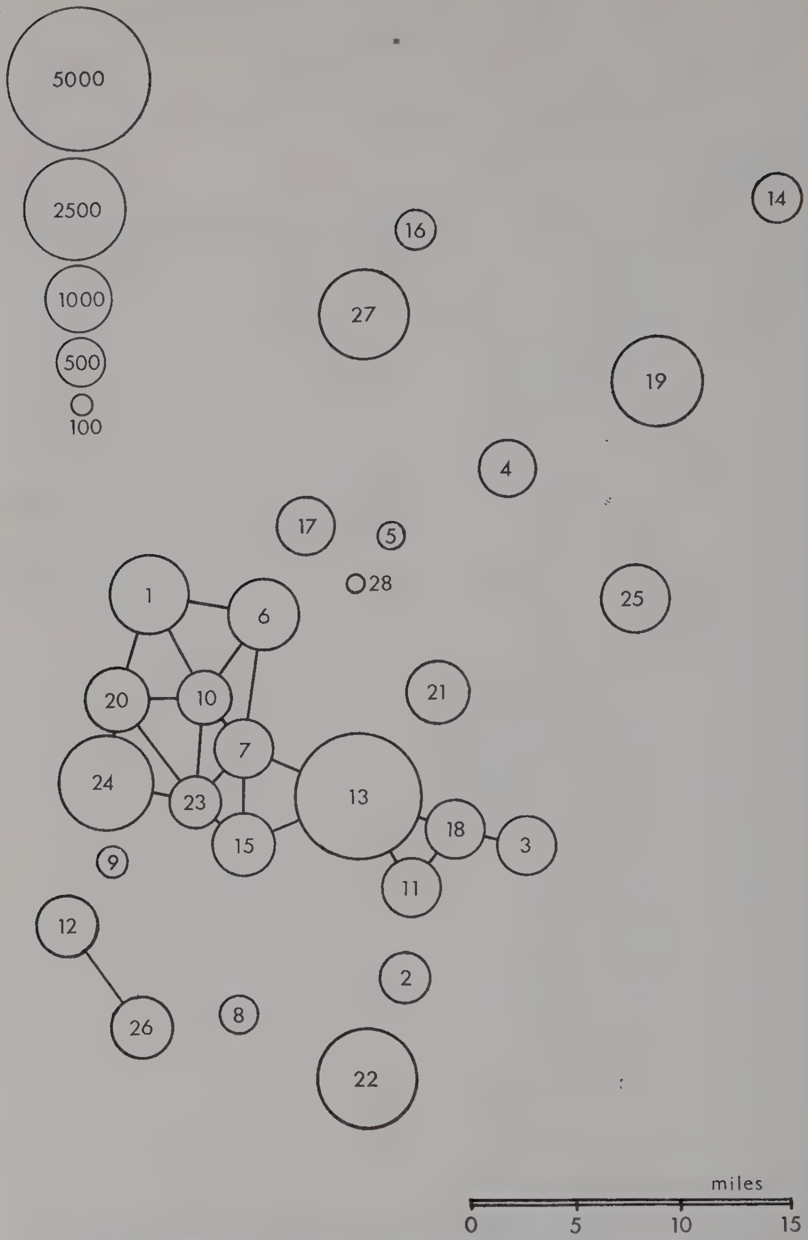

FIG. 2. Sizes of parish populations in 1861. Connected circles represent mainland parishes. Area of circles proportional to numbers of inhabitants.

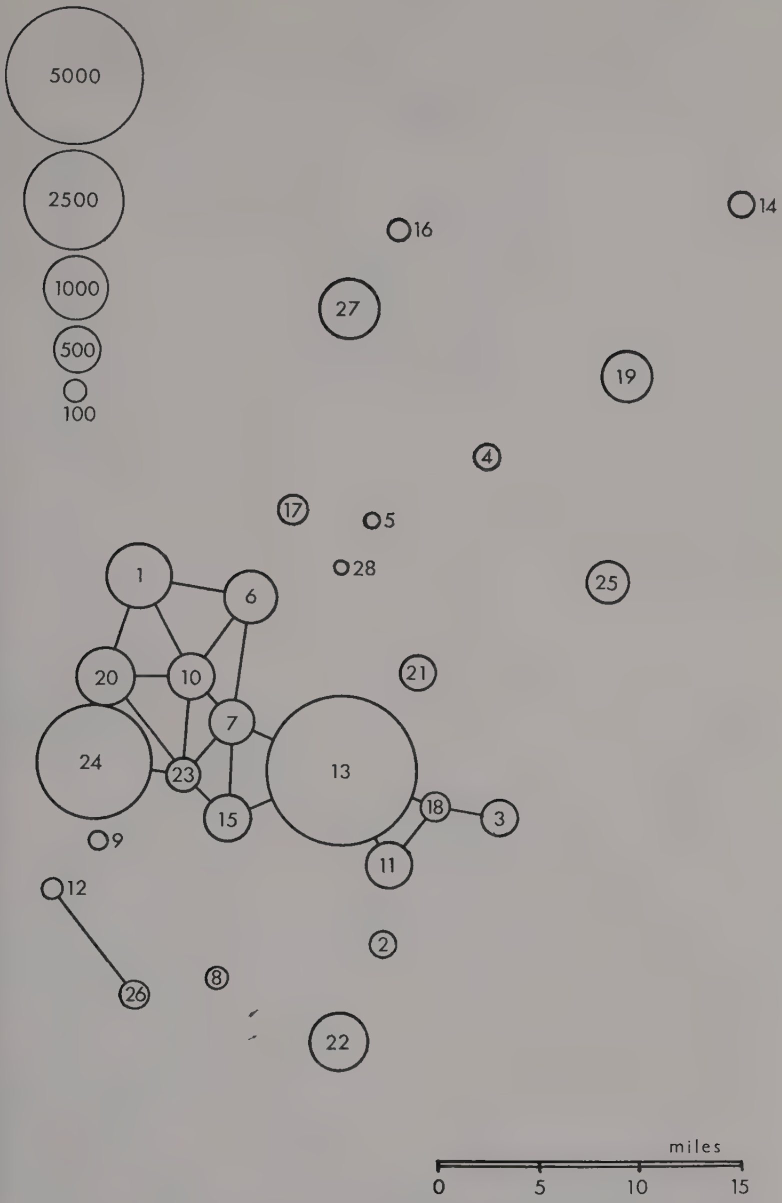

FIG. 3. Sizes of parish populations in 1961.

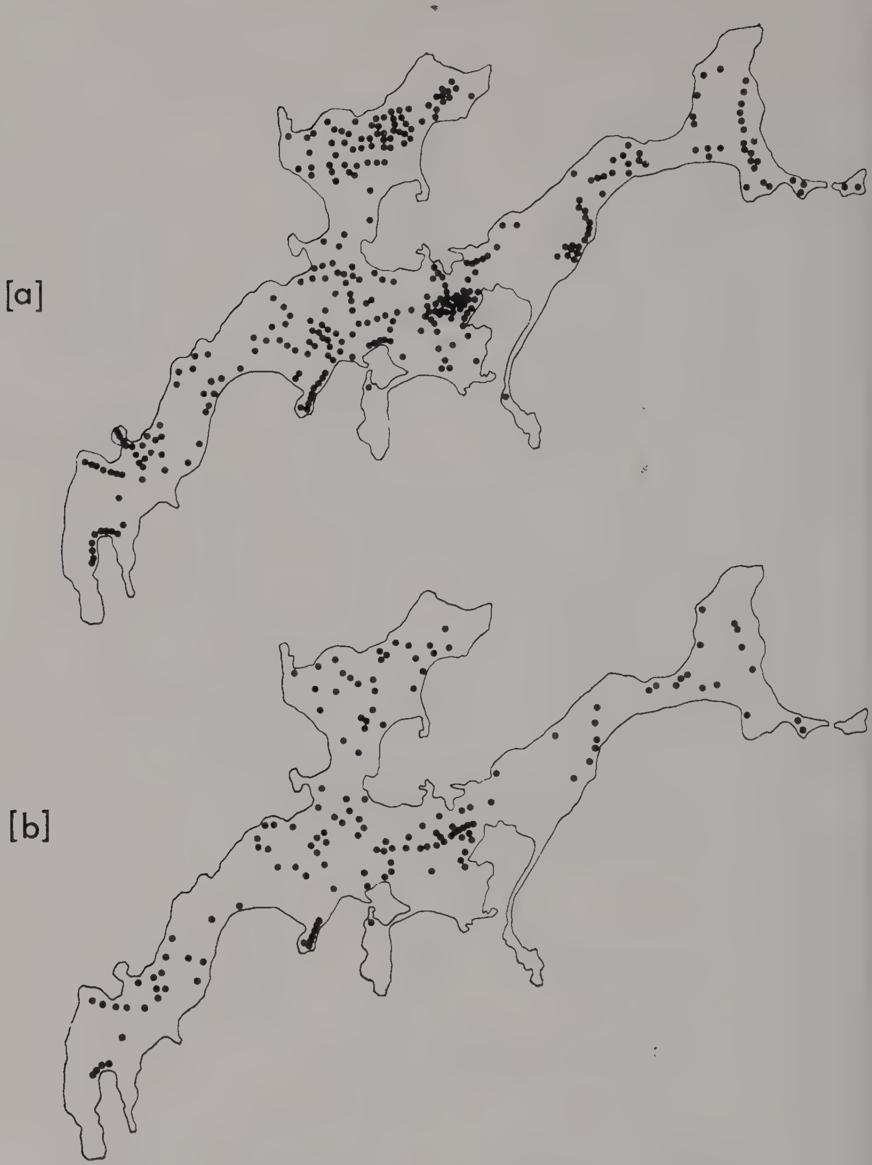

FIG. 4. Spatial distribution of houses on the island of Sanday. (a) in 1905. (b) at the time of the survey in 1971.

degrees of isolation from one another, provides an opportunity of investigating the interplay of evolutionary factors in producing genetic variation, in particular the factors of population size and patterns of movement.

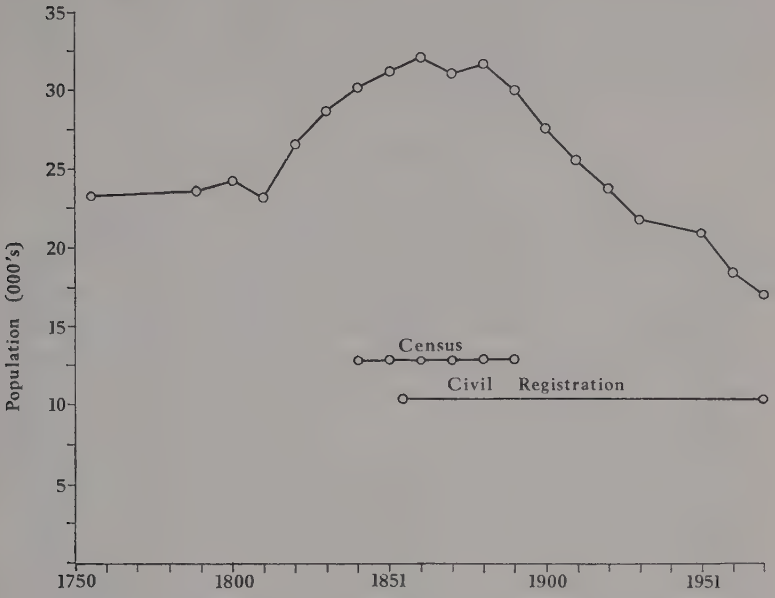

FIG. 5. Population of Orkney Islands (1755–1971) and time spans of Census Returns and Civil Registrations available for analysis.

The investigation of the genetic and demographic structure of the population is greatly helped by the availability of excellent records. The time spans of the two main classes of these are shown in Fig. 5. The Enumerators' Returns for the Decennial Censuses, available from 1841 to 1891, provide information about inhabitants at a single point in time; the Civil Registrations of Births, Marriages and Deaths give details for individuals in approximately four generations since 1855.

In addition to their value for micro-evolutionary studies, the Orkney Islands form an ideal situation for regional studies. They represent a community of manageable size for investigation and, unlike much of the rest of Britain in which there has been extensive movement of people and urbanization, they are a community in which there has been comparatively little change in way of life for many generations, and which is isolated from the rest of the country. They provide an opportunity of adding to the information about regional variation in this country, and of investigating the relationship with those parts of Scandinavia from which the Norse colonists came, and with other places, for example Iceland, Greenland, Shetland, in which the Norse settled.

The Survey

Most studies of genetic variation in this country use suitable "captive" samples, such as hospital communities, or members of the armed services. An examination of the general population is obviously difficult and time consuming. Two strategies have been adopted in the present survey: the first is house to house visiting, in which arrangements are made for volunteers to attend at a survey centre. Using this method, which enables a local community to be studied, response rates of about 40 per cent have been obtained. The second approach involves the examination of schoolchildren. The method of organization of secondary schools on the islands means that each school contains children whose parents live in a variety of different parishes. By means of these survey methods, 820 individuals have been studied since the survey was started in August 1970. The sample consists of two local groups—the northern island of Sanday (19 on Fig. 1) and the mainland parish of Deerness (3), and schoolchildren from Kirkwall (13) whose parents live mostly in the central and eastern parts of the Mainland and the northern islands, and from Stromness (24) whose parents live in the west Mainland and the southern islands. Temporary visitors to the islands, or children whose parents were temporary visitors, were not included but no attempt was made to exclude close relatives. Instead, genealogical information was collected from individuals and from civil registers to enable relationships to be established.

Traditionally, a large number of characters has been included in regional surveys, but the genetic basis of many of these is poorly understood. As the main purpose of this survey is to make genetic comparisons with other communities, and to study evolutionary factors, the survey has concentrated mainly on characters with a simple genetic basis to their variation; for example, those provided by blood and saliva samples, and by tests of colour and taste discrimination. In addition, the polygenically determined variation in finger and palm prints has been examined.

One of the more popular general beliefs concerning the Vikings and the members of Norse communities is that they were tall and blond; and variation in eye and hair colour, and in anthropometric characteristics has also been studied. However, until the genetic basis of this variation is more fully understood, its use as an indicator of either local or geographical relationship must be made with caution.

Examples of Variation

Full analysis of the material and information collected is still in progress but even preliminary results give clear indications that considerable differences exist between the Orkney Islands and the rest of Britain, and that there is local variation between the island communities themselves.

Blood Antigens

Most published data for British and other European populations on any scale are for the ABO and Rhesus (D) systems, and this is true for the Orkney population. However, work in progress by various groups (for example, in addition to our own work, surveys by the North and North East Scotland Regional Blood Transfusion Services, and by the London Hospital) should soon provide data for many polymorphic systems in Orcadians. Here, only the ABO system is considered. Allele frequencies for various British and European populations are shown in Table 1, which includes the results of the present survey and a previous survey by Brown (1965). There is considerable heterogeneity in the ABO frequencies among northern European populations. The Danish and Norwegian populations, however, are both characterized by high A allele frequencies. If gene frequencies in modern Scandinavian populations are used to estimate frequencies in early Norse populations, then the frequencies in Orkney, Shetland and Iceland, each of which has a considerable Norse element, are surprisingly low, although they are higher than those found in other parts of Scotland. Regions in other parts of Britain with relatively high A frequencies do correspond to some extent to regions of Viking settlement (see, for example, Watkin, 1956 and 1960) but it seems more likely (Fisher and Taylor, 1940; Steffensen, 1953) that the proto-Scandinavian groups were characterized by relatively low A allele frequencies and are sharply distinguished from the modern Scandinavian peoples, which have changed greatly by infiltration from central and eastern Europe since the Viking period. The use of ABO frequencies as indicators of relationships with Scandinavian communities must await much more detailed studies of local variation in gene frequencies, particularly in those areas from which the original Norse settlers are thought to have originated.

TABLE 1. ABO gene frequencies for various British and other European populations

Population	Sample size	Gene frequencies (%)		
	N	p	q	r
Iceland				
(Donegani, *et al.*, 1950)	878	19·15	7·03	73·82
Denmark				
(Goldschmidt, 1961)	87920	27·82	7·46	64·72
Norway				
(Hartmann and Lundevall, 1944)	4972	30·44	5·52	64·04
Shetland				
(Brown, 1965)*	146	18·99	8·62	72·39
Orkney				
(Present study)	407	18·37	11·68	69·95
(Brown, 1965)*	154	22·92	11·25	65·82
North-East Scotland				
(Kopeć, 1970)	1092	19·25	10·22	70·53
Rest of Scotland				
(Kopeć, 1970)	53675	21·65	7·09	71·26
Wales				
(Kopeć, 1970)	16273	25·25	6·95	67·80
England				
(Kopeć, 1970)	397385	26·19	5·89	67·92

* Gene frequencies recalculated by Bernstein's method (Bernstein, 1930) from phenotype frequencies given by Brown to ensure consistency with other gene frequencies given in the table.

The high frequencies in the B allele, noted by Brown in north-east Scotland and in Orkney, are shown also by the present results. The exceptionally high B frequencies found in Orkney distinguish the islands not only from more southern areas of Britain, but also from other areas of Norse settlement, such as Shetland and Iceland.

It will be possible to investigate the causes of these high frequencies when more information on variation within the Islands is available.

Taste and Colour Blindness

Sunderland, in his review (1966) of the frequencies of phenylthiocarbamide non-tasters in the United Kingdom, gives mainland frequencies of non-tasters which range from 27·6 per cent (N=1005) in south Wales to 32·0 per cent (N=206) in Scotland. In a sample of 420 Orcadians, however, he found 37·7 per cent non-tasters, with even higher frequency (41·5 per cent) in those members of the sample from the northern islands, although only 41 individuals were in this category. In the 567 individuals so far tested as part of the present survey, such high frequencies were not found, although the frequency of non-tasters (32·6 per cent) is higher than the frequency for Scotland given by Sunderland. With relatively small samples, the difficulty of precise establishment of the anti-mode, and the possible inclusion of relatives, leads to considerable problems in determining non-taster frequencies and in testing the significance of differences between frequencies. However, the results of both the present survey and Sunderland's earlier survey point to the conclusion that the Orcadians have higher frequencies of non-tasters than other populations in the British Isles.

The prevalence of colour blindness was investigated by means of Ishihara plates. Administration of these to 404 males and 416 females, indicated frequencies of overall "red-green" colourblindness of 5·20 per cent and 0·72 per cent respectively. Post, in a review (1963) of colour blindness frequencies in Britain, found evidence of declining frequency of colour-blindness from south to north and from west to east. His overall frequency for the East of Scotland, based on 6236 subjects is 4·92 per cent (compared with a high frequency of 9·27 per cent for south-west England, based on 6648 subjects). Although the present figure is in close agreement with that found by Post, it is doubtful if it provides further evidence for the "relaxation of selection" hypothesis. Adam (1969) has argued that the contention that high rates of red-green colour blindness are due to relaxed selection is inconsistent with much population data, and that discussion of selection and its relaxation should be based on studies differentiating mild from severe effects. Such studies require an anomaloscope, and unfortunately it has not yet proved possible to include the use of an anomaloscope in the present survey. If, however, it could be shown that it is the severer, dichromatic defects which are at a lower frequency in Orkney, this would support the relaxation hypothesis.

Dermatoglyphics

There is as yet little information on regional variation in finger and palm print characteristics. Holt (1964) gives digital pattern frequencies for 1000 unrelated individuals ("most of whom were resident in London or the surrounding counties") and Cummins and Midlo (1943) cite frequencies for 5000 male individuals from Scotland Yard records. Data for the four Orkney samples and the overall Orkney frequencies are compared with these general samples in Table 2.

TABLE 2. Fingerprint pattern frequencies (%) in Orkney and other British populations

Population	N	Whorls	Ulnar loops	Radial loops	Arches
Sanday	217	27·1	59·7	5·5	7·7
Deerness	127	25·6	61·5	5·0	7·9
Stromness	202	25·9	62·5	5·0	6·6
Kirkwall	238	27·3	62·9	4·4	5·4
Total Orkney	784	26·5	61·7	5·0	6·8
Britain					
(Holt, 1964)	1000	26·1	63·5	5·4	5·0
(Cummins and Midlo, 1943)	5000	25·4	64·0	5·7	4·9

The most marked difference between the Orkney and rest of country samples is in the frequency of whorls and arches. The increase in arch frequency is particularly evident in the more isolated communities of Deerness (parish 3 on Fig. 1) and Sanday (19). As might be expected, the proportionately higher frequency of arches is reflected in lower total ridge counts. These vary between 115·2 and 114·6 for males (Holt, 1964, gives a mean for 825 males of 145·2) and between 126·0 and 106·4 for females (Holt gives a mean for 825 females of 127·0). The variation of ridge counts within samples, measured by the standard deviation, is not appreciably different from that found by Holt (Orkney values from 43·0 to 60·9, Holt's values 51·1 and 52·5). There are significant differences between islands in mean total ridge count, and the high heritability of this character, and the ease

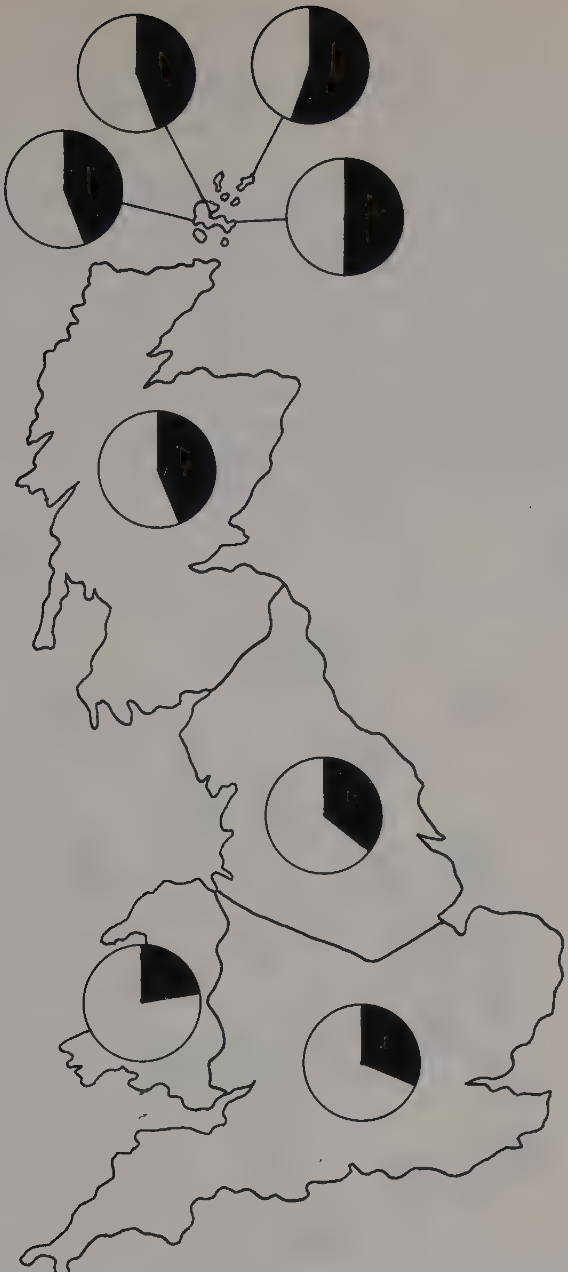

FIG. 6. Proportions (shaded areas of circles) of grey, intermediate, dark- and light-blue eyes (Martin categories 12, 14–16) for Orkney and other areas of Britain.

with which it can be determined, make it a suitable basis for detailed inter-island comparisons which are now in progress.

Pigmentation

Although detailed spectrophotometric study of the Orkney hair samples is not complete, a simpler colour-matching of the specimens into six divisions demonstrates clearly that about 60 per cent of the specimens display the two darkest degrees of hair colour, and only about 2 per cent show marked blondness. In contrast, very high frequencies of grey, intermediate, dark- and light-blue eyes (Martin categories 12, 14, 15, 16) were found, with the highest frequencies in the most northerly sample (the island of Sanday, 19). In Fig. 6, data for Orkney are compared with Grieve and Morant's figures (1946) for Scotland, Wales and north and south England.

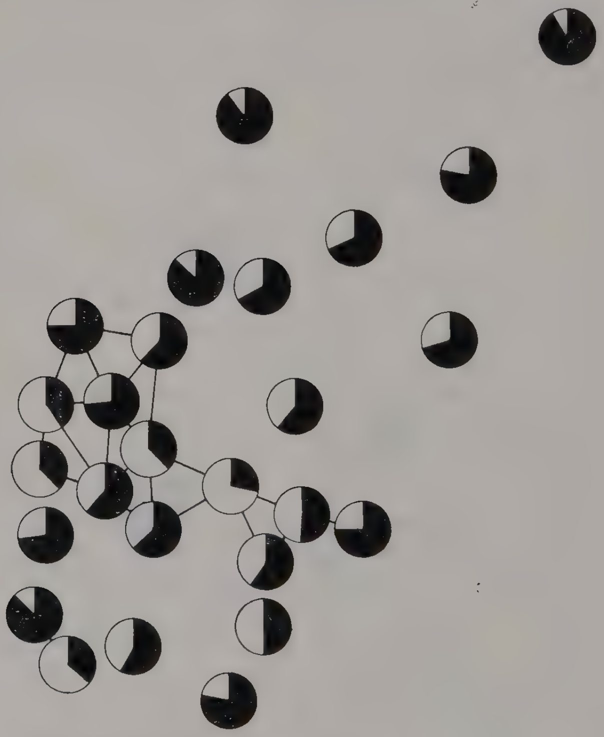

FIG. 7. Proportions (shaded areas of circles) in 1861 of married male heads of households living in parish of birth.

Population Structure

An understanding of the significance of the similarities and differences between Orkney and other populations, and among the various Orkney communities can only be achieved through the study of the origins and inter-relationships of the inhabitants. Until the advent of permanent, systematic records of individuals, the historical information is necessarily imprecise. Clearly, however, more detailed investigation of the relative contributions of the settlers through the three main phases of Orkney history will help in determining affinities with other communities.

Variation between the island communities, however, is likely to be influenced by more recent factors, particularly those of small population size and patterns of movement between communities

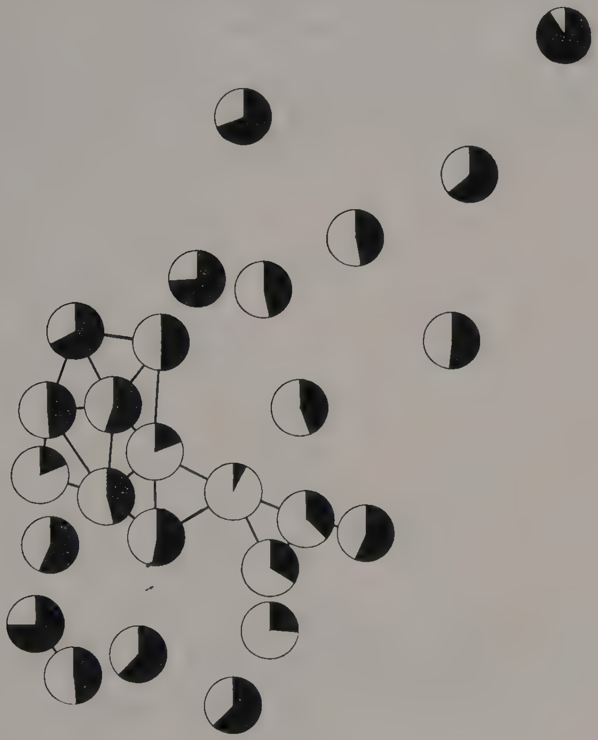

FIG. 8. Proportions (shaded areas of circles) in 1861 of marriages in which both partners were born in same parish.

(Harrison and Boyce, 1972) and these can be investigated through the study of demographic records. The Census Enumerators' Returns in Scotland are available from 1841 to 1891. These returns provide information on household composition, and on the ages, marital condition, occupation, and birthplaces of inhabitants. A number of parameters of genetic importance can be determined from these records, in particular the effective sizes of populations and their degrees of isolation and interconnection. For example, an indication of the degree of isolation of a community can be obtained by examining the proportion of individuals living in the community who were born there. An alternative approach is to examine the proportion of marriages which are endogamous, that is in which both partners are from the same community. Examples of these two approaches are given in Fig. 7 and Fig. 8. In both cases, there is very considerable variation in the degree of isolation of the various communities, with the northern islands showing most, and the mainland parishes showing least isolation. The two largest communities, Kirkwall and Stromness are the most open.

In Scotland, access to Civil Registrations on a geographical basis is possible, in contrast to the situation in England and Wales.

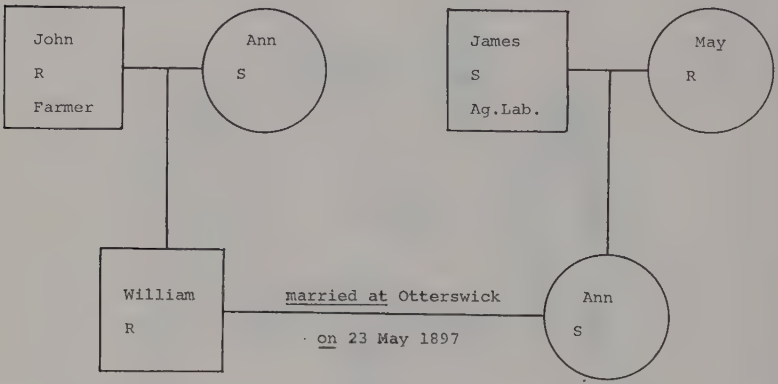

FIG. 9. Information about William R——l and his wife and their immediate relatives provided by his birth (B), marriage (M), and death (D) certificates.

B: born at Clickimin on 25 June 1862 at 0500, vaccinated on 12 August 1862

M: living at Myre, age 34, bachelor, married Ann S——r, living at Otterswick, age 18, spinster; married at Otterswick 23rd May 1897

D: died at Myre on 23 November 1922 of pneumonia

Although these records, which begin in 1855, do not go as far back into the past as Church records, they are an informative record, in a standardized form, for all inhabitants, not only those of a particular religious denomination. Figure 9 indicates the wealth of information about an individual (in this case one William R——l) and his wife and their immediate relatives that is provided by his birth, marriage, and death certificates. Information from these records permits more detailed investigation of parameters of genetic importance. An example of the kind of information of genetic significance provided by, for instance, the marriage records is given in Fig. 10, which shows the distribution of distances between places of residence of

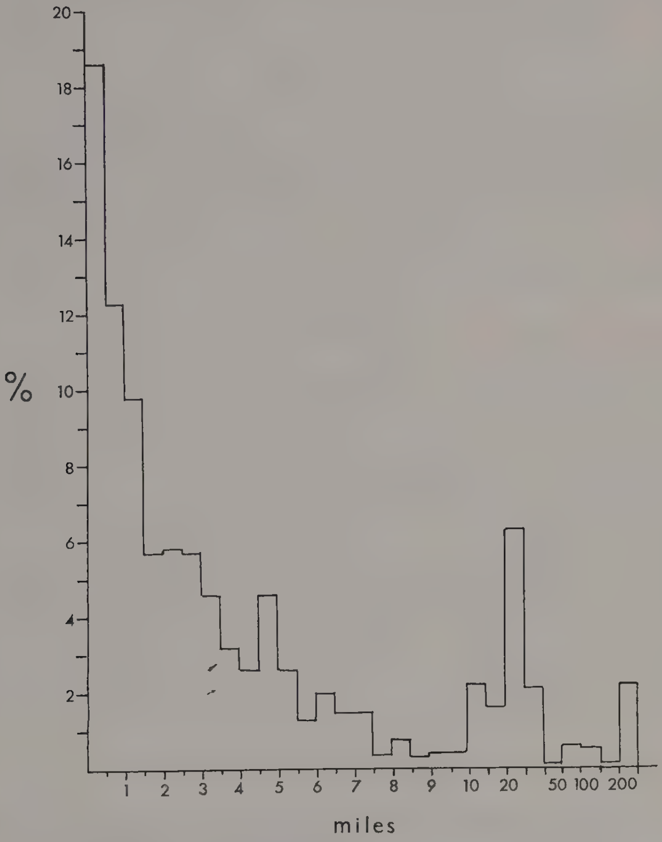

FIG. 10. Distribution of distances between residences at time of marriage of husbands and wives marrying on Sanday between 1855 and 1965.

husbands and wives at the time of their marriage on the island of Sanday, totalled over the years 1855 to 1965. It shows first how very skewed the distribution of marriage distances is, and that the indications of isolation provided, for example, by endogamy rates, do not disclose the very short distances over which most marriages occur. For the island of Sanday, only a small proportion of spouses comes from outside Orkney (3·4 per cent) or even from outside the island (15·5 per cent) and of those marriages which are endogamous, nearly 75 per cent are between people living within three miles of one another.

The small effective population sizes and the relatively short distances over which movement of genetic significance occurs suggest that stochastic processes may well have played an important part in producing local genetic variation. Information from civil registers, and from census returns, about all components of movement, can be summarized in the form of migration matrices (Bodmer and Cavalli-Sforza, 1968; Hiorns, Harrison and Boyce, 1969) the analysis of which enables predictions to be made of patterns of relatedness and of genetic variation. It is the purpose of work now in progress to compare the predictions of these models with observed patterns of variation.

Conclusion

The Orcadians have a strong sense of identity and provide an example of a distinctive rural community, isolated from the rest of the British Isles. In a number of genetically determined characters they vary from communities in other parts of the country. Further investigation is now needed to determine the extent to which these contrasts are the result of the complex historical origins of the Orkney people. There is also genetic heterogeneity within the Orkney Islands, and the geographical isolation and structure of the islands, and the nature and organization of the demographic records of the area, provide an excellent opportunity of testing models which attempt to explain local genetic variation in terms of population sizes and patterns of movement between populations.

Acknowledgement

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Mr. A. Bain, past and present Director of Education for Orkney, and Dr. I. Haddow, Chief Medical Officer for the county. The headmasters of the Stromness Academy, Kirkwall Grammar School, and Sanday School were particularly helpful during the work with children. We should also like to acknowledge with thanks all those who have taken part in the survey so far, and to all parents who have permitted their children to be examined. Last, but not least, our thanks to those who have helped either during field work or in processing information, particularly Dr. Carol Cowell, Dr. Hilary Hubbard, Don Tills, Elaine Cadbury, Anita Williams, Elizabeth Park, Theresa Goodman, Susan Bradley, Anthony Hopkins, Jenny Boore and Theya Molleson.

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BLOOD GROUP DISTRIBUTIONS IN BRITAIN

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It is now a little over fifty years since Professor and Mrs. Hirszfeld first showed that blood group frequencies varied widely between human populations. This discovery gave to anthropology a new criterion for the classification of human individuals and populations, and one that was, in many respects, more efficient than those formerly accepted: morphological characteristics such as proportions of the skull, texture of the hair or colour of the skin, which are not susceptible to clear-cut sub-division and, moreover, their genetics even at the present time are not wholly understood. They are also liable to modification by the environment.

When the Hirszfelds made their observations, the ABO blood groups were the only ones known. Since then, another 10 major blood group systems have been discovered and subsequently, many systems of plasma proteins and red-cell enzymes. Each of these systems has the advantage of clearly separable classes and simple genetics, most of the types vary markedly in frequency from one population to another and some systems even have certain alleles the presence or absence of which has racial connotation, thus adding valuable characteristics for the differentiation of human populations. Nevertheless, observations on the ABO groups are still by far the most numerous, both with regard to the number of racially or geographically defined sets and with regard to the number of individuals tested, and their world distribution is the most fully known.

This preponderance of observations within the ABO system is, of course, due mainly to the world-wide necessity of supplying blood for transfusions, and the records of each blood collecting organization are at the same time a treasury of genetical information. One of the principal tasks of the Serological Population Genetics Laboratory (formerly the Nuffield Blood Group Centre) was to use that information for the study of one genetical system in the United Kingdom, and the execution of that task was made possible by the full cooperation of the Regional Centres of the National Blood Transfusion Service. From the eighteen such Centres in Great Britain we received, over a period of about ten years, copies of the cards made out for *new* donors reaching a total of nearly half a million, or about 1 per cent of the population. For Northern Ireland we had the opportunity of examining the records for the whole panel (both Live and Resigned), a total of over 66,000, i.e. about 5 per cent of the population. All these data were classified according to the private address of the donors. For this purpose we used the scheme of the General Post Office, which met our requirement of making the size of the topographic units depend upon the density of their population. For the final comparison some of those initial units were joined to adjacent ones so as to reach a minimum of 100 donors per area, leaving 1096 areas in Great Britain and 60 in Northern Ireland.

The statistical analysis of such a large number of population samples might perhaps show that they did not differ more than would be expected by pure chance or, if there were marked differences, that the variation was quite erratic. Two large-scale surveys carried out before ours was started made either of those outcomes unlikely. In 1940, Fisher and Taylor examined the extensive data of the emergency blood transfusion service, dividing the country into three regions, Scotland and England north and south of the Humber. Their results showed that O decreased and A increased from north to south, and that B was higher in Scotland while it did not differ in the two English regions. As the borders of the regions were laid down a priori, the course of the variation was not known nor whether there were any changes within each of the regions. In 1953, however, Dr. Fraser Roberts carried out a very detailed analysis of the data for donors registered with the Regional Centre of Newcastle-upon-Tyne. The region concerned covers Cumberland, Westmorland, Northumberland, Co. Durham and the northern part of the North Riding of Yorkshire. It was shown that this whole large area could, with regard to the A/O ratio, be divided into two parts, each homogeneous *within* itself while all the heterogeneity was *between* them.

This result for the North of England clearly formulated the question we were trying to answer for the whole country: could it be divided into a number of areas satisfying those same conditions, i.e. being internally homogeneous and significantly differing from the adjoining ones? The maps show that such a division was made and what the results were. As the variation of O and A is largely reciprocal, the maps for A are given here; B and AB were added together throughout the analysis and are shown together on the maps. The figures printed on each map are the phenotypic frequencies, i.e. A/N and B+AB/N and the regions provided with such a figure and covering most of the country are those that seem to define the rule of variation. The smaller areas marked by dotted lines are the local exceptions to that rule. The detailed data are set out in Kopeć (1970).

Results

For the variation of A (Fig. 1) the increase from north to south is confirmed and that from west to east established; the highest A is, however, reached in the northern part of East Anglia, and Peterborough.

Now for the exceptions: Glasgow and the remainder of Lanarkshire have A/N = 31·97; that is much lower than the rest of Scotland except that northern part for which we have data. In the large region that has A/N = 41·09, there are insets where it is markedly higher: they are Shipley, Bingley and Ilkley (A/N = 45·61), Todmorden (A/N = 52·97) and, adjoining it, Barnsley, Halifax and Huddersfield (A/N = 43·11) and, finally, the central part of Sheffield (A/N = 45·61). There is also one inset where A/N is much lower, 37·80, and that is Liverpool. In the general region that has A/N = 42·57, there is Warwick and Shipston-on-Stour where it is 51·09. In Wales it is interesting to note that Pembrokeshire plus the town of Cardigan has the highest A/N found anywhere consistently over a whole series of unit areas; it is 47·40. In the area immediately to the east, it falls to 40·48. The still lower value of 37·60 covers most of Wales but the eastern part of Glamorgan and most of Monmouthshire have the higher A of a large part of central England. The London Postal Area (i.e. all the numbered districts) was, of course, highly heterogeneous but it separated surprisingly easily into 3 areas. Of those, two are similar to the adjoining counties; most of S.E. and much of E. and N. agree with south-eastern England; all S.W.

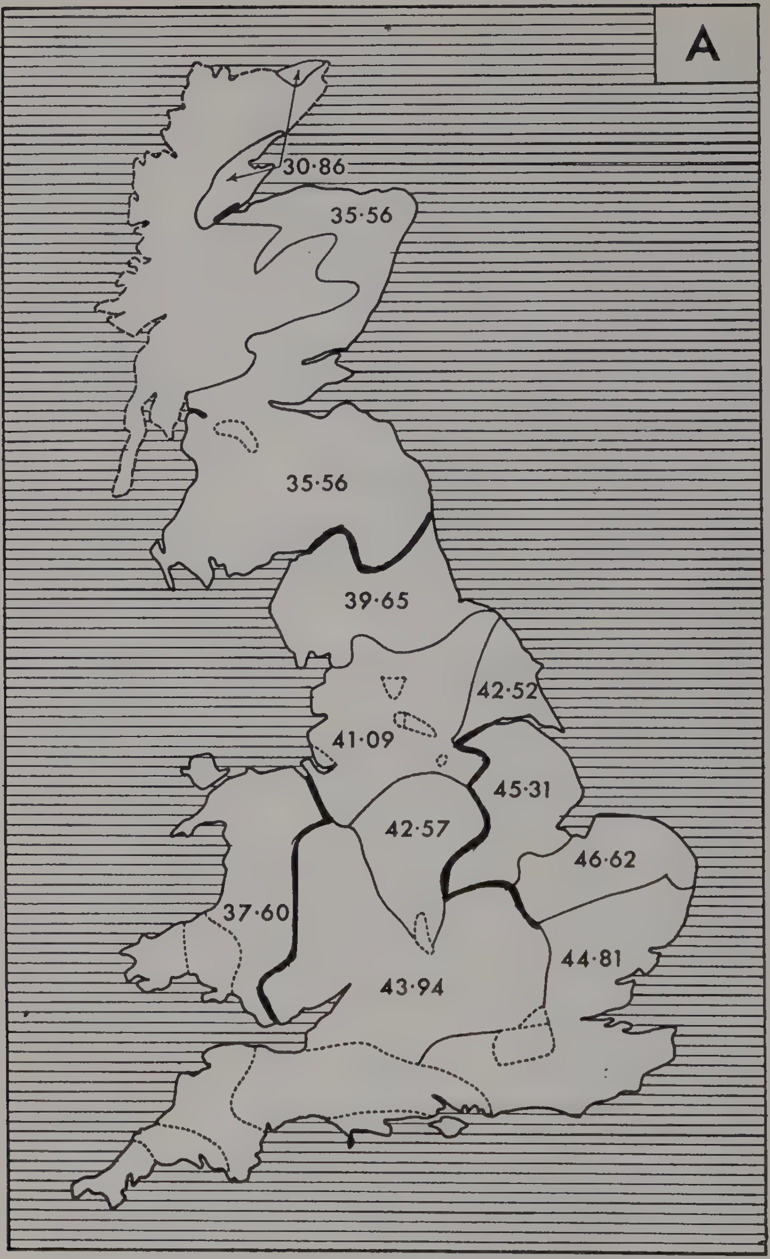

FIG. 1. After Kopeć (1970) by permission of Oxford University Press.

districts that are south of the river and the remaining ones of S.E. have, as has Surrey, markedly lower A. On the other hand, what is roughly the western half of London north of the river differs strongly and in all respects from all that surrounds it; A is lower still and B higher. With the distribution of A in south-western England I have had more difficulties than with any other region; whether the more erratic variation there is really due to the populations, or whether our particular set of data is simply awkward for no good reason, I cannot say. The best sub-division I could think of produces 5 areas, three of which agree with the general trend of increasing A, being interrupted by two where A is much lower.

The variation of B+AB is smaller in numerical range and the "final" areas satisfying the conditions are fewer (Fig. 2). A higher frequency consistently exists in Scotland (with an even stronger rise in the extreme north), in most of Northumberland and in Wales including adjoining parts of Cheshire and Lancashire. The lowest frequencies are found in Cumberland, Westmorland, parts of Co. Durham, of the North Riding, of Cheshire and Lancashire and in East Anglia and Essex. All the rest of England with the exceptions of the few local insets has uniform frequencies between 11 and 12%. The exceptions are part of Co. Durham with Middlesbrough, the southern part of the Furness, Preston, parts of the North and West Ridings, one part of Liverpool, Norwich, Beccles and Bungay and, as already mentioned, part of London.

Combining the outcomes of the comparisons of B+AB, A and O, the whole country has been divided into 39 areas, each of which is homogeneous with regard to all three of the ABO types considered and differs significantly from all adjoining ones with regard to at least one of them.

Discussion

At this point, one question is bound to be asked and I want to anticipate it: are those results the only ones that could be obtained from our data or, if not, are they the best ones? My answer to the first part of that question is in the negative and I cannot answer the second part! Yet, this is less discouraging than it sounds.

I don't want to go here into the details of the statistical method I used but in essence it consists of finding a set of χ^2's that satisfies the required conditions. The calculations were done by me and not

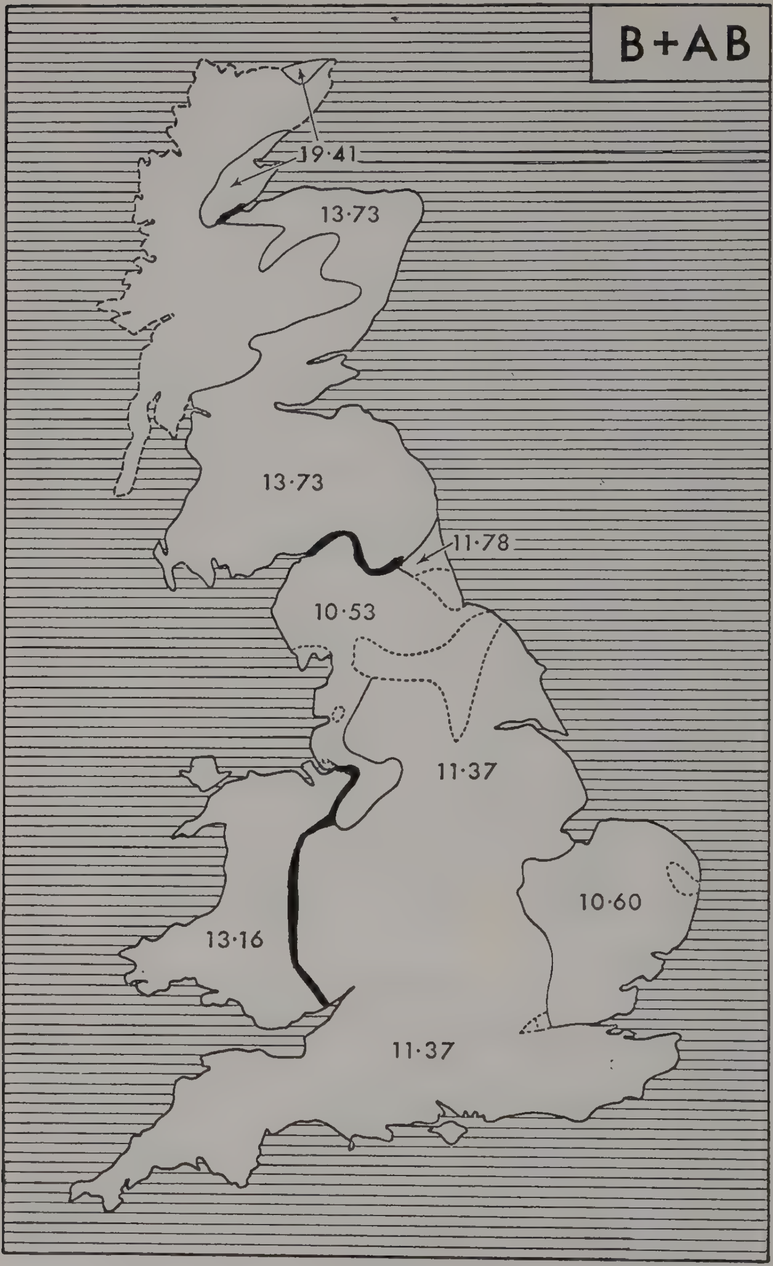

FIG. 2.

by an electronic computer and even I have found more than one acceptable set; of these, I have chosen the best one but I have not tried all possible ones. Also, of course, completely different methods of analysis might have been used on the same data and possibly will be. Yet, I do not think that the resulting picture would be substantially different from the one I have obtained. Moreover, my many trials and hesitations have suggested to me a certain way of interpreting my results.

Formally, of course, each of the dividing lines I have drawn has the same status, which is that the populations on either side are unlikely to have been sampled from the same parent-population. A significant χ^2 tells no more than that. Yet, are we to believe that the variation is discontinuous everywhere? I don't really think so and I would qualify my lines according to the greater or smaller facility of determining them and also to the difference of the resulting frequencies. Sometimes a number of unit-areas could be transferred and hardly change the χ^2's or the frequencies, sometimes again, the transfer of just one of them would affect both considerably. I suggest that only in the latter case do we really have a sudden change while in the former the variation is, in fact, gradual.

The insets or "patches" (marked in dotted lines) belong, of course, to the second category, as they were picked out because they were different. Of the others I think only those marked with thick lines show an abrupt change.

The value of anthropological conclusions to be drawn from my results depends upon the correctness of two assumptions: that donors are random samples of the local population and that such a population is, genetically, characterized by its habitat.

The first is, I think, no longer under doubt for the ABO groups. In the early days of blood transfusion there was the statistical danger that donors were selected in favour of group O. Now, however, O is no longer considered the "universal" donor group and recipients are given blood of their own group, so that there is no need for donor selection. In this country, also, there is no risk of a certain social selection of donors such as may exist in countries where blood is being paid for, where I have seen people described as "professional" donors.

The second query may be put this way: could not separate samples of one population defined by its geographical location differ between themselves more than is explained by chance using the standard conventions? That point is vital and I have tried to check upon it. This was made possible by the fact that I have been receiving my data in separate batches over a period of ten years. I have routinely compared successive samples from the same regions and not found more variation than would be expected on a random basis.

Further reassurance on both points was also furnished by the data on nearly 50,000 Air Force recruits which we were able to examine owing to the courtesy of Air Vice-Marshal Stamm. These recruits are of course selected for age and sex and, possibly, some other factors but, even so, no consistent differences between them and the donors have emerged.

Another fact relevant in this connection is that my line in the north of England is very similar to that found by Dr. Fraser Roberts (with nearly identical frequencies north and south of it), even though we were working on different data and used different unit areas and a different method of comparison.

I have also tried to test our material for the possibility of variation in time by comparing, for the final regions, data recorded before and after what was, roughly, the midpoint in time of our survey. The outcome of this comparison may also have some bearing on the anthropological interpretation of our results. For neither O nor A was there marked variation; for B+AB, on the other hand, there was a consistent change. Out of the 39 final regions, that frequency has increased in 26 and had our survey stopped after the first half, a much larger part of the country would have been, with regard to B+AB, in the lowest frequency class. If just ten years could produce such a difference, it could easily be imagined that longer ago, the gene B was rarer in all England than it is now. It is also interesting that the strongest increase during our period of observation was in Birmingham and an extensive part of London.

That change seems interesting for the following reason: perhaps the main cause for variation of the genetical structure of a population is the influx of another one completely different; as far as ABO blood groups are concerned, it is less easy to trace back the reasons for variation of O and A, their frequencies varying widely all over the world. The distribution of B, on the other hand, is much easier to define; in Europe, its frequencies increase steadily from west to east, and, except perhaps for the Basques, are lowest in England. Going into Asia, they continue to increase reaching their highest values in India and Pakistan. With the exception of American Indians and

Australian Aborigines, all non-European races have much higher frequencies of B. Thus, all likely immigrants to this country will tend to raise the frequency of that gene.

For most of my other observations on the variation of ABO blood groups in this country, be it the clear gradient or the abrupt changes, I must leave it to specialists to find the explanations; only in a few cases can I suggest one myself. The lower A in Glasgow and Liverpool is due to the Irish in the former, to the Irish and Welsh in the latter. In both cities, I have segregated our material by family names and have found very significant and consistent differences. For London, inspection of Census results has proved that in the two areas that agree with the adjoining counties, the frequency of people born outside the British Isles or born in Scotland, Wales and Ireland is roughly the same as it is in the respective counties. In the remainder of London, that is the area which is different with respect to all the blood groups, the frequencies of both classes of immigrants are much higher.

Northern Ireland

I have left the mention of my observations in Northern Ireland quite separate because it is part of a separate island and because our data from there were received in a different form. My methods of analysing them were, however, quite the same as for Great Britain and my results are presented in the same way, i.e. marking the abrupt changes by the thicker line.

Looking at the map for A (Fig. 3), it can be seen that areas 30·59 and 29·34 (i.e. all Tyrone and much of Derry, including the city of Londonderry and the southern part of Co. Down) differ but little between themselves while they differ significantly from the regions lying between them. They also do not differ from the nearest counties of the Irish Republic for which I quote Dawson's (1964) data: there Louth has A = 30·70 and Donegal 30·81. The two regions marked 35·82 (Fermanagh and all Armagh except Lurgan) do not differ at all, they differ very markedly from all the rest of Northern Ireland and as strongly from their neighbours in the Irish Republic. Monaghan lying between Fermanagh and Armagh has A = 28·65, Cavan and Leitrim which abut upon Fermanagh have respectively 30·46 and 29·55.

With regard to B + AB (Fig. 4), the sub-divisions differ only in two points from those obtained for A. In the north, the decrease of

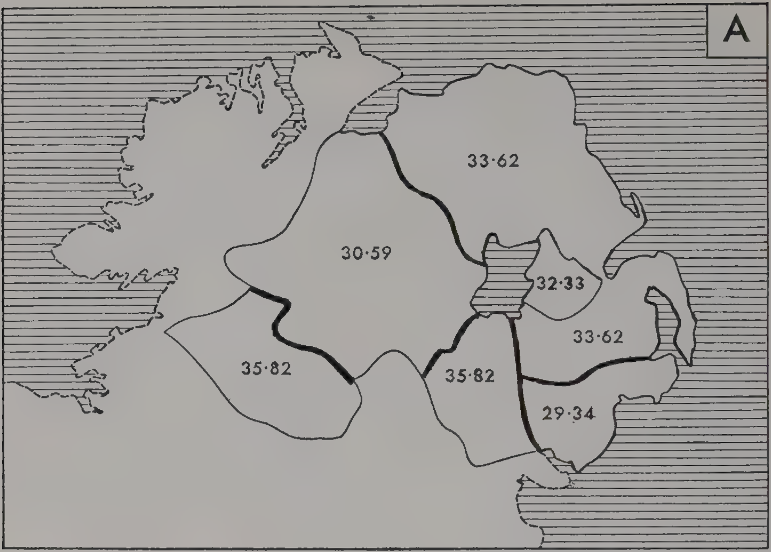
A
33·62
30·59
32·33
33·62
35·82
35·82
29·34

FIG. 3.

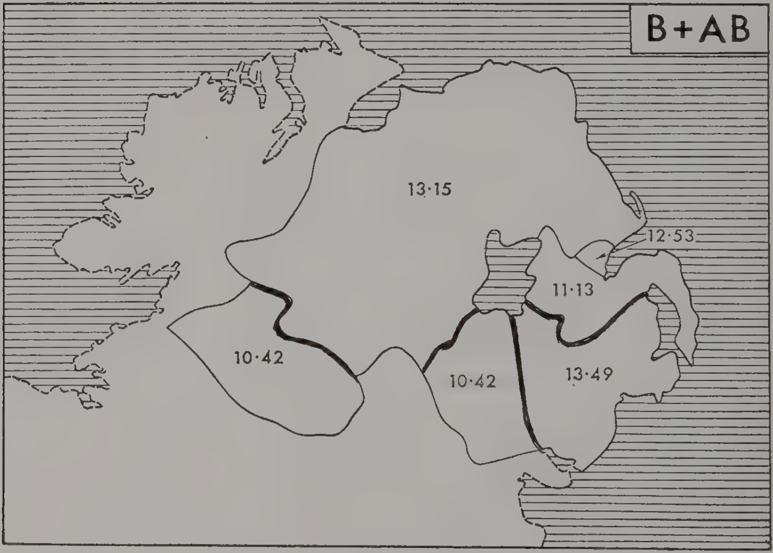
B+AB
13·15
12·53
11·13
10·42
10·42
13·49

FIG. 4.

B+AB seems more gradual and its sudden increase in Co. Down does not coincide with the abrupt decrease of A in the same county. For B+AB also, Fermanagh and Armagh are completely different and the frequency of that group is exceptionally low there. Dawson shows lower frequencies in the five counties of the Irish Republic adjoining Northern Ireland but none as low as that, none even as low as 11·13 which I find for southern Co. Antrim, part of Belfast and the north of Co. Down. As cards for the whole Resigned Panel (more than half of my total) were only lent to me and had to be dealt with quickly, I could not check upon family names which might have been useful.

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GENETIC STUDIES IN IRELAND

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THE idea of studying the genetic constitution of the Irish people has particularly interested one of the authors (D. Tills) for some time. A county by county survey was started in 1969 in collaboration with the Blood Transfusion Services of the Republic and Northern Ireland. Blood samples were obtained from more than 2000 blood donors and these were examined for over twenty distinct genetic systems. Although the hoped-for total of 100 individuals from each county was not attained, more than fifty samples were obtained in most cases. Arising from this preliminary work, in 1970 an International Biological Programme (Human Adaptability Section)/Royal Society Expedition led by E. Sunderland carried out further investigations in Southern Ireland and some of the findings are reported upon here.

Chadwick (1970) writes "There is no doubt that Ireland as a whole is an extremely conservative country, and the nearest we can ever hope to attain to the original Celtic people. Despite later invasions, it has to a great extent been left behind by time, and we can there study something of the ancient Celtic world". Chadwick was principally thinking of literary and cultural rather than genetic legacies. However, when the Celtic-speaking invaders arrived they almost certainly absorbed a large pre-Celtic population and thus a cultural survival of "the ancient Celtic world" probably means also a biological survival of pre-Celtic genes.

Surprisingly little research has hitherto been carried out on the physical and genetical features of Irish populations. Apart from the work of Hooton and Dupertuis (1955) for continuous polygenic factors, virtually all the data collected have been confined to ABO and Rh (D) typing. Some more intensive work has been carried out in Northern Ireland and particularly by Casey *et al.* (1963, 1969) and Bajatzadeh *et al.* (1969) in small areas in the Republic.

The Irish Population

Ireland has witnessed a relatively small influx of peoples in historical times. Most of the incursions, other than those of the Vikings, have been due to the plantation policies of the English crown. The Anglo-Norman invasion of 1169 probably only involved some 1000 men. Though the plantation policy as such started under the Tudors, at that time only small numbers were involved. Small groups were placed in Leix and Offaly in the 1550's and others in Munster in the 1580's. After the flight of the Earls in 1607 a more sustained effort was made to plant the six counties of Armagh, Cavan, Donegal, Derry, Fermanagh and Tyrone in the province of Ulster. Some of the settlers came from England but the vast majority were from the Scottish lowlands. This policy continued under Cromwell and to a lesser extent under William III also. Its effect on the population structure of Ireland may well have been exaggerated. Certainly figures based on land ownership, showing that Catholic holdings dropped to one seventh of their original value, give an erroneous impression as much of the land was transferred to Protestants of Irish descent and not to fresh settlers.

Apart from such known movements of peoples, other factors render the history of the population of Ireland unique in Europe. In the early nineteenth century a large population explosion occurred in Ireland. Whilst the population of Ireland was estimated to number some five million in 1800, by the 1841 census the total had increased to over eight million. It seems that the population almost doubled during a period of less than a century from a probable four million or so in the middle of the eighteenth century to the 1841 census figure.

It is interesting, though perhaps not entirely justifiable, to speculate that this virtual doubling of the population resulted in increased genetic diversity within the population. Ford (1965) suggested that large population increases would result in greater variability, and that forms would survive which would be eliminated under less favourable conditions. Admittedly it is dangerous, however interesting, to translate ideas founded on studies of Lepidoptera to human situations.

This increase in population size was directly related to and sustained by the introduction of the potato into Irish husbandry and when the potato crop failed the population came under great stress. In the period 1845–1848 a partial and later a complete failure of the potato crop occurred due to blight, and this resulted in the last great famine in a West European country. The number of individuals who died as a result of this has been put as high as two million but one million seems a more likely figure. Among the main causes of death was "Famine fever" which include the two diseases, typhus and relapsing fever. Other causes of death were dysentery, scurvy and starvation. Darlington (1969) suggests that the population was probably halved by the twin agencies of death and continued emigration.

Several migrations had occurred previously from Ireland, notable amongst which was the "flight of the wild geese" in 1691. However, all previous emigrations were insignificant compared with that initiated by the famine. This wave of migration started in July 1846 and by June of the following year 300,000 had landed in the port of Liverpool alone. In 1847 over 100,000 migrants sailed for Canada.

It is therefore interesting in the light of this unique population history to attempt to see if any of the known genetic factors show significant differences from those available for the rest of Europe, and if so to what extent, if at all, they can be attributed to Celtic ancestry or ascribed to the population disaster which occurred over 130 years ago.

The 1970 Expedition

During the 1970 expedition it was planned to collect genetic data from the populations in several different parts of Ireland. The three areas selected are as follows (Fig. 1)

1. Carnew, a small township in Co. Wicklow, South East Ireland. This is mainly a granitic area.
2. Rossmore, Co. Cork, South West Ireland. This is principally an area of shales and sandstones.
3. Ballinlough, Co. Roscommon, North West Ireland, principally an area of limestone.

These three locations are widely separated from one another and each is predominantly rural. If genetic heterogeneity exists within the Irish population then aspects of this heterogeneity might well be revealed in three such sample populations. In total over 700 individuals participated in the investigation, the majority of whom took part in the full survey procedures.

The blood samples collected during the 1970 expedition were tested for most of the genetic factors used in the major study started

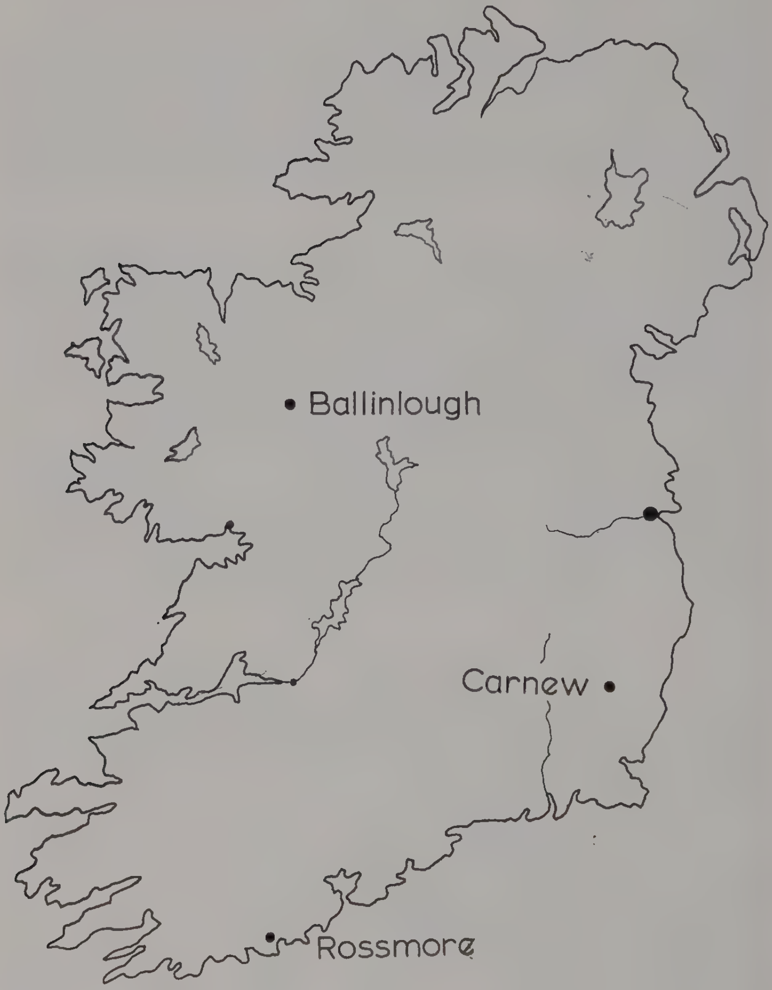

FIG. 1.

in 1969 to which reference has been made. Although the 1969 data are still being processed they have been used for comparative purposes, subject to the usual qualifications.

The 2000 individuals who participated in the 1969 survey are very much more numerous than those involved in the 1970 Expedition. However the three regions selected for study in 1970 are far better represented than they were in the 1969 survey. Thus in 1970, 175 blood samples were obtained in Carnew but only 58 for Co. Wicklow and 54 for Co. Wexford in 1969. Again the 157 individuals obtained in Rossmore compare favourably with the 76 for Co. Cork as do the 158 for Ballinlough with the 60 for Co. Roscommon. In the 1969 survey as with many other surveys using blood transfusion donors, the average frequency of Rh (D) negatives is higher at 20 per cent than the 16 per cent found in randomly selected individuals. From a cursory glance at the data it would appear that the *O* gene frequency may also be slightly higher in the 1969 survey. With these qualifications in mind the information can yet be used for comparisons with the 1970 Expedition material.

Serological Results

ABO Groups (Table 1)

The frequencies found both in the 1969 and the 1970 series are very similar to those obtained by Hackett and by Dawson. Hackett (1958) using ABO data showed that the *A* gene frequency was higher in the Eastern (planted) counties than in the Western ones.

Table 1. Percentages of ABO blood group gene frequencies

	Carnew	Co. Wicklow	Rossmore	Co. Cork	Ballinlough	Co. Roscommon	Ireland
p_1	12·8	15·1	13·5	15·1	9·7	18·7	12·5
p_2	6·1	3·6	3·8	5·5	7·4	2·6	4·5
q	7·7	6·3	7·3	4·0	8·6	10·7	6·8
r	73·4	75·0	75·4	75·4	74·3	68·0	76·2

This he thought was due to plantation as it was likely that the early Irish and Vikings had similar ABO gene frequencies. He estimated that the proportion of Anglo-Norman and plantation mixture was 1 : 6 in the Republic as a whole and as high as 1 : 2 in Dublin. Dawson (1964) agreed with these results, but extended and confirmed the pattern of higher B in the central and south west counties of the Republic which showed a sharp discontinuity at the Boundary of the ancient province of Ulster. The 1969 and 1970 surveys corroborated the lower frequency of the A gene in the west. The higher B gene frequency in the south west and central counties is not as clear as that obtained by Dawson but this is probably due to the smaller sample size. If the frequencies for the A_1 and A_2 genes are added together the frequencies for the towns and counties fit well into the overall Irish pattern. There is however a marked difference between the Ballinlough and Co. Roscommon data. It seems likely that this is a sampling effect, since Co. Roscommon has a higher A and lower O gene frequency than any of its neighbouring counties. Mourant (1954) commenting on an A_2 frequency of 9·5 in Dublin wondered if this gene had a high frequency throughout Ireland. The present figure for Dublin is 4·5 and the data for the rest of the country are similar to those for the remainder of the British Isles.

MNSs Groups (Table 2)

The total MNSs complex frequencies are very similar to those reported for England. Ikin *et al.* (1954), who tested only 106 specimens, found the MS complex to be lower and the Ms higher for Northern Ireland than those in England. It has not been possible to confirm this; the Northern Ireland frequencies in the 1969 survey are very similar to those found for the rest of Ireland.

TABLE 2. Percentages of MNSs blood group gene combinations

	Carnew	Co. Wicklow	Rossmore	Co. Cork	Ballinlough	Co. Roscommon	Ireland
MS	19·3	27·5	25·9	26·2	26·0	27·7	26·8
Ms	33·6	34·6	37·8	23·9	34·8	26·5	29·3
NS	5·5	2·7	2·4	6·4	3·7	2·4	5·8
Ns	41·6	35·2	33·9	43·5	35·5	43·4	38·1

With the exception of the rather aberrant Carnew findings, the data fit well into the British pattern. The Carnew sample shows a higher Ns and a lower MS frequency than expected, a tendency which is not seen in any of the neighbouring counties and which clearly requires further investigation.

Rh. Groups (Table 3)

The Irish have the rarer Rh complexes present in frequencies similar to those expected for a western European country. The data in the table require clarification. Some of the differences are undoubtedly due to sampling effects, particularly the R_2^U frequency in Co. Wicklow. This is also illustrated by the absence of R_0 from the small county samples, although it reaches and exceeds its expected frequency in the larger samples from the towns.

TABLE 3. Percentages of Rh blood group gene combinations

	Carnew	Co. Wicklow	Rossmore	Co. Cork	Ballinlough	Co. Roscommon	Ireland
R_1	45·5	48·3	40·8	42·1	41·4	40·3	38·12
R_2	13·6	13·2	12·7	20·4	20·9	18·9	15·47
R_1^W	1·1	0	0·6	0	1·0	0·8	1·11
R_1^U	0·8	0	2·1	0	0	2·3	0·50
R_2^U	1·0	4·0	0	0	0	0	0·30
R_Z	0	0	0	0	0	0	0·02
R_0	2·8	0	1·6	2·8	3·3	0	1·38
r^1	0	0	1·4	0	0	0	0·38
r^{11}	0	0	0	0	0	0	0·36
r	35·2	34·5	40·8	34·7	33·4	37·7	42·36

Huth *et al.* (1953) carried out tests on 200 individuals and reported frequencies (excluding the R_0^U figure) similar to those found in the present surveys. No tests were carried out by Huth for the C^W antigen. These Irish frequencies differ from those of England in that the *cde* complex is slightly higher. The R_1 frequencies for the counties surveyed are higher than most of the rest of Ireland but this probably has little if any significance.

Dawson found that a higher frequency of Rh (D) negatives occurred in the same areas as those showing an increase in the *A* gene, that is, the "planted areas". Preliminary study of the 1969 data tends to confirm this finding and showed that the increase in Rh (D) positives in the west consists of both R_1 and R_2, although the increase in the R_2 levels appears greater.

The C^W frequencies found are very similar to those reported for other parts of the British Isles and Europe. The remainder of the data conform fairly well with the pattern for the whole of Ireland outlined above. There are two exceptions; the *cde* frequency for

Co. Wexford appears to be excessively high, although not as high as the 53 per cent for nearby Co. Carlow. The R_2 frequency for Co. Cork is also high but is similar to that found for the neighbouring county of Tipperary. Other adjacent counties show frequencies more in accord with those found for Rossmore.

Other Blood Groups (Table 4)

The Lu^a frequencies on average are lower than those for the rest of Western Europe. There is, however, a very wide range from 4 per cent in Co. Leix to 0 per cent in Co. Derry but there is no easily discernible pattern of distribution.

TABLE 4. Percentages of other blood group genes

	Carnew	Co. Wicklow	Rossmore	Co. Cork	Ballinlough	Co. Roscommon	Ireland
Fy^b	63·7	60·3	62·4	60·0	53·6	65·8	58·4
Lu^a	1·2	3·5	1·9	3·4	0·7	0	1·9
K	5·1	1·7	3·8	6·7	2·9	4·2	4·4
P_1	49·3	47·5	40·6	46·7	37·6	46·0	48·1

The *Kell* frequencies are approximately the same as for the rest of the British Isles. No high frequencies similar to those reported by Casey in Co. Cork were detected. Some Kp^a positives were detected but these were never found in K positives and the numbers were small as is the case for almost all European populations tested for the Kp^a antigen.

The Fy^b frequencies ranged from 70 per cent in Co. Kerry to 45 per cent in Counties Longford and Offaly but on the whole they still fit into the European pattern.

With the exception of the level at Ballinlough all the P_1 gene data obtained are close to those found in the British Isles and Western Europe generally.

Protein and Enzyme Variants (Table 5)

The frequencies shown for the haptoglobin (Hp^2), phosphoglucomutase ($PGM_1{}^2$) and the acid phosphatase genes P^a and P^c are almost identical with those derived from the small number of populations tested in other parts of Europe. The frequencies for the adenylate kinase (AK^2) and 6-phosphogluconate dehydrogenase (PGD^C) genes are slightly lower and those for the adenosine deaminase (ADA^2) higher than other European values. The ADA^2 figure for Co. Cork is very high and with that for Co. Tyrone was the highest found in either of the Irish surveys as well as being the highest so far reported in Europe.

TABLE 5. Gene percentages—protein and enzyme variants

	Carnew	Co. Wicklow	Rossmore	Co. Cork	Ballinlough	Co. Roscommon	Ireland
AK^2	2·6	5·0	1·6	4·6	1·3	1·5	3·5
PGD^C	1·7	4·4	1·0	0·6	1·3	1·5	1·5
Hp^2	54·9	57·6	57·8	66·5	59·8	68·9	62·0
$PGM_1{}^2$	23·3	32·7	24·4	27·8	23·4	21·2	25·0
							$PGM_1{}^6$
$PGM_1{}^7$	0·3	0	0·7	0	0·3	0	0·05
P^a	34·5	31·9	30·8	30·5	31·3	34·1	33·7
P^c	4·0	6·9	7·4	4·6	2·8	3·8	4·5
ADA^2	6·6	7·0	5·8	11·0	7·0	5·6	5·6
Tf^B	0·3	0	0·4	0·7	0	0·8	1·0

There are two further points of interest in the enzyme tests carried out in the two surveys. Firstly in the major survey no examples of the rare $PGM_1{}^7$ gene were found whereas it was found in all three samples obtained in 1970. Secondly although no examples of the variants of the enzyme LDH were detected in the 1970 material they did occur in the 1969 group at a very low level. In fact variants of this enzyme are absent from nearly all populations so far tested or else only occur at very low levels. The variant detected in Ireland was also found in Iceland (Mourant *et al.* 1968) and it is of interest in regard to the history of the two countries that this should be so.

Conclusions

With the exceptions already mentioned the data presented here show that the Irish people have gene frequencies that place them well within the usual Western European patterns. The higher frequencies of the *O* and Rh (D) positive genes found in the west are probably due, as Mourant has suggested, to populations being forced westward from the United Kingdom and Eastern Ireland by successive waves of migration.

As stated earlier this is only a preliminary assessment of the information but so far it has not revealed any great differences which could be ascribed to Celtic ancestry, nor has it revealed any

TABLE 6. Distribution of samples by P.T.C. taste threshold

	Carnew		Rossmore		Ballinlough	
	Males	Females	Males	Females	Males	Females
Non tasters	10	14	14	6	19	13
1	18	23	10	11	14	12
3	1	10	7	2	5	8
4	3	3	3	0	4	1
5	6	3	7	2	3	1
6	1	9	6	4	9	5
7	36	64	25	31	29	37
9	25	27	33	20	24	48
11	3	8	4	8	3	2
Total	103	163	109	84	110	127
Non tasters (Antimode 4)	$\frac{30\cdot5}{103}=29\cdot61\%$	$\frac{49\cdot5}{163}=30\cdot37\%$	$\frac{32\cdot5}{109}=29\cdot82\%$	$\frac{19}{84}=22\cdot62\%$	$\frac{40}{110}=36\cdot36\%$	$\frac{33}{127}=26\cdot38\%$
Male + Female	$\frac{80}{266}=30\cdot08\%$		$\frac{51\cdot5}{193}=26\cdot68\%$		$\frac{73\cdot5}{237}=31\cdot01\%$	

TABLE 6 (*continued*)

	All males (C+R+B)	All females (C+R+B)	All ♂+♀ (C+R+B)
Non tasters	43	33	76
1	42	46	88
3	13	20	33
4	10	6	16
5	16	6	22
6	16	18	34
7	90	132	222
9	82	95	177
11	10	18	28
Total	322	374	696
Non tasters (Antimode 4)	$\frac{103}{322}=31\cdot99\%$	$\frac{102}{374}=27\cdot27\%$	$\frac{205}{696}=29\cdot45\%$

alterations in gene frequencies of a kind which might have occurred during the phase when the population was increasing rapidly. If this population increase, famine and large scale emigration have altered the gene patterns this has either been corrected, or the various forces involved have cancelled each other out, or the gene distribution has moved to one that corresponds to that of Western Europe.

P.T.C. Tasting

P.T.C. taste testing was carried out on some 700 individuals using the modified, eight solution version of the Harris-Kalmus (1949) testing procedure. As for all the survey procedures details of the ancestry of every participant were ascertained and the great majority of those included in the regional samples claimed long established local ancestry. Virtually all the grandparents of those examined were of local origin and in many cases, particularly at Carnew, localized ancestry could be traced back for five or even more generations. Inevitably as a consequence some of those who constitute the samples are more or less closely related but since the three samples represent no more than a fraction of the local population it is impossible to estimate the total magnitude of the intermarriage and inbreeding. From extensive pedigrees collected in Carnew there is direct evidence of a high degree of inter-relatedness among participants in the survey. This was less evident in the other two localities visited. It would be especially interesting to complete the Carnew genealogies.

In recent years work done on PTC tasting in various parts of the British Isles has demonstrated significant regional differences (Cartwright and Sunderland 1967). However there was a paucity of Irish material and an attempt was made to provide some useful data. The results are summarized in Table 6.

The male and female nontaster frequencies for Rossmore and Ballinlough, the antimode being taken at Solution 4, appear to be very different: 29·82 per cent for males and 22·62 per cent for females in Rossmore; 36·36 per cent for males and 26·38 per cent for females in Ballinlough. Yet in neither of these regions nor in Carnew was a significant sex difference established at the 5 per cent level of probability, using χ^2 (Table 7). Therefore males and females were combined in each of the three regions, giving nontaster percentage values of 30·08 in Carnew, 26·68 in Rossmore and 31·01 in Ballinlough.

Again, using χ^2, no significant regional heterogeneity was demonstrated. For 322 Irish males, the nontaster frequency is 31·99 per cent; for 374 females, the frequency is 27·27 per cent. The male and female sample of 696 individuals provides a value of 29·45 per cent nontasters.

TABLE 7. Ireland—P.T.C.

χ^2 comparisons of taster and non taster frequencies in Irish populations

				χ^2	1 degree of freedom
Carnew	Males	C/F Carnew	Females	0.0171	N.S. (0·50–0·90)
Rossmore	Males	C/F Rossmore	Females	1·2561	N.S. (0·10–0·50)
Ballinlough	Males	C/F Ballinlough	Females	2·7472	N.S. (0·05–0·10)

For 1 degree of freedom 5% Probability level = 3·84
For 1 degree of freedom 10% Probability level = 2·71

No sex differences

Comparisons of frequencies among males of Carnew, Rossmore and Ballinlough	2 degrees of freedom
$\chi^2=1\cdot4623$	N.S. (0·10–0·50)
Comparisons of frequencies among females of Carnew, Rossmore and Ballinlough	
$\chi^2=1\cdot7335$	N.S. (0·10–0·50)
Comparisons of frequencies among males and females combined of Carnew, Rossmore and Ballinlough	
$\chi^2=1\cdot0248$	N.S. (0·50–0·90)

For 2 degrees of freedom 5% probability level = 5·99
For 2 degrees of freedom 10% probability level = 4·61
No geographical differences

Skin Colour

Percentage reflectance values were obtained using an EEL spectrophotometer. Three filters, 601, 605 and 609, with dominant wavelengths of 425, 545 and 685 mμ were utilized in obtaining readings on the medial aspect of the upper arm.

Table 8 summarizes the results obtained for males and females separately. At virtually all wavelengths for each of the three areas the female readings are higher than those for the males. The one

TABLE 8. Ireland skin colour

Reflectance values at 425 mμ, 545 mμ and 685 mμ. Medial aspect of upper arm							
Males							
	n	Mean 425 mμ (601)	Standard deviation	Mean 545 mμ (605)	Standard deviation	Mean 685 mμ (609)	Standard deviation
Carnew, Co. Wicklow	105	34·86±0·43	4·36	39·37±0·43	4·36	64·40±0·34	3·52
Rossmore, Co. Cork	111	34·63±0·39	4·13	40·72±0·40	4·26	64·69±0·30	3·13
Ballinlough, Co. Roscommon	105	35·40±0·42	4·30	40·94±0·41	4·17	65·31±0·32	3·30
Females							
	n	Mean 425 mμ (601)	Standard deviation	Mean 545 mμ (605)	Standard deviation	Mean 685 mμ (609)	Standard deviation
Carnew, Co. Wicklow	162	37·23±0·33	4·17	42·12±0·32	4·01	64·64±0·22	2·85
Rossmore, Co. Cork	90	35·66±0·43	4·05	41·81±0·44	4·15	64·75±0·35	3·29
Ballinlough, Co. Roscommon	127	36·19±0·34	3·78	41·90±0·32	3·60	65·13±0·23	2·58

exception is the reading at 685 mμ for the Ballinlough males, which is fractionally higher than for the Ballinlough females.

An analysis of variance was carried out for each of the three filters separately. The results are different in each case. For filter 601 both sex and location have significant effects; for filter 605 there is an interaction between these effects and neither is significant when tested against the interaction; for filter 609 only the variation between locations is significant (Table 9).

TABLE 9. Analysis of variance. Carnew, Rossmore and Ballinlough data

Source of variation	Sum of squares	D.F.	Mean square	Variance ratio
	Filter 601			
Between sexes	356·6	1	356·6	23·46
Between locations	107·2	2	53·6	3·53
Interaction	87·3	2	43·7	2·87
Within sub-groups	10549·0	694	15·2	
	Filter 605			
Between sexes	472·2	1	472·2	—
Between locations	39·8	2	19·9	—
Interaction	121·0	2	60·5	4·58
Within sub-groups	9165·9	694	13·2	—
	Filter 609			
Between sexes	0·36	1	0·36	<1
Between locations	58·56	2	29·28	9·69
Interaction	5·23	2	2·61	<1
Within sub-groups	2097·28	694	3·02	—

Filter 601

The interaction mean square is not significant at the 5% level and so the "within sub-groups" mean square may be used to test for significance between sexes and between locations. The male mean is 35·02 and the female mean is 36·46 giving a difference of 1·44 which is significantly different from zero ($p<0{\cdot}001$). The difference between locations is also significant ($p<0{\cdot}05$). Values of t for differences between individual locations are as follows: Carnew and Rossmore 2·65, Carnew and Ballinlough 1·07, Rossmore and Ballinlough 1·59 so that the difference is significant only between Carnew and Rossmore.

Filter 605

The interaction mean square is significant at the 5 per cent level, indicating that the difference between males and females depends on the location. It is not permissible to use the "within sub groups" mean square to test for significant effects due to sex and location, but the interaction mean square may be used. Neither effect is found to be significant (the male and female means are 40·33 and 41·99 respectively). We may, however, use the within sub-groups mean square as the variance estimate for each sub-group and perform t-tests between male and female. The difference in Carnew is significant at 0·001 ($t = 6 \cdot 04$) and Rossmore and Ballinlough give values of 2·11 and 2·00 respectively which are both significant ($p < 0 \cdot 05$). It is of course the large sex difference for Carnew in comparison with the others which produces the significant interaction.

Filter 609

Since the interaction is not significant we may test the main effects using the mean square for "within sub-groups". The sex difference (males 64·79, females 64·83) is not significant. The difference between locations is significant ($p < 0 \cdot 001$). The values of t for differences between pairs of locations are: Carnew and Rossmore 1·09, Carnew and Ballinlough 4·30, Rossmore and Ballinlough 2·94 and so the location effect is mainly due to the high Ballinlough values.

Others in this symposium report upon their skin colour studies in other parts of the British Isles, including Cumbria, the Isle of Man, South Wales and Northumberland. We do not wish at this stage to comment upon their results although they are all broadly similar and constitute useful representative samples of British populations. However some other, published, comparative results are available. (Table 10). Harrison and Owen's (1964) data are not strictly speaking comparable since they combined both male and female data in a single set of reflectance values. Again Barnicot's results (1958) were obtained from a different part of the body—the flexor surface of the right forearm—and this site may well provide markedly different percentage reflectance values compared with the medial aspect of the upper arm.

Leguebe (1961) and Rijn-Tournel (1966) have each published data for Belgians and their reported mean reflectance values are, by and large, considerably higher than those found among the Irish. Ojikutu (1965) provides data for a mixed European male series and

TABLE 10. Skin colour. Percentage reflectance values. EEL spectrophotometer. Medial aspect upper arm

Population	n	425 mμ (601)	545 mμ (605)	685 mμ (609)
Males				
Carnew, Eire	105	34·86	39·37	64·40
Rossmore, Eire	111	34·63	40·72	64·69
Ballinlough, Eire	105	35·40	40·94	65·31
Belgium (Leguebe 1961)	143	37·71	44·77	67·27
Belgium (Rijn-Tournel 1966)	68–69	39·12	43·80	64·51
Mixed Europeans (Ojikutu 1965)	74	40·3	45·2	66·9
Females				
Carnew, Eire	162	37·23	42·12	64·64
Rossmore, Eire	90	35·66	41·81	64·75
Ballinlough, Eire	127	36·19	41·90	65·13
Belgium (Leguebe 1961)	177	36·50	44·57	65·88
Belgium (Rijn-Tournel 1966)	45–46	38·18	43·15	63·65
Males and females combined				
Europeans including many Irish (Harrison and Owen 1964)	46–105	36·1	41·0	62·3
Flexor surface right forearm				
Europeans (mainly English) Barnicott 1958 M	50	32·8	37·9	61·5
F	50	34·3	40·5	63·1

again the reflectance values are well above the Irish figures. It is interesting to note that both in Leguebe's and in Rijn-Tournel's data the males are lighter skinned than the females whilst the reverse is true in Ireland.

Summary

Results on serological gene frequencies from a sample of some 500 subjects, and on PTC tasting ability and skin colour on some 700 subjects from three localities in Ireland are given. Skin colour shows differences between localities, which appear to be supported by some serological gene frequency differences, for which a historical explanation is suggested. In general, the Irish gene frequencies fit well into those usual for western Europe.

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TILLS, D. PhD Thesis (In preparation)

THE INCIDENCE OF SOME GENETIC MARKERS IN IRELAND

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As part of an extensive anthropological survey of northern Europe, one of us (J.P.) carried out anthropological field-work in Ireland, namely in Dublin, Cork, Killarney, Tralee, Limerick, Galway, Ballymahon, Longford, and Roscommon. One object of these investigations was to get reliable anthropological data, on which to base discussion of the supposed genetical relationship of the populations of Ireland and Iceland. Various historical and anthropological aspects of this question have been discussed previously by Palsson (1967). During this field-work in Ireland (1967–68) when blood samples were collected, there was excellent cooperation with the Irish. The results are published here in order to extend knowledge of the incidence of the genetic markers tested by us in the Irish, and to allow comparisons to be drawn between the Irish data and those obtained in other European populations, especially in the Icelanders.

Material and Methods

Our total sample consists of 295 unrelated adult males, aged from 20–30 years. They originate mainly from the middle-west of Ireland, Galway, Cork and its vicinity, and a few from Dublin (Figure 1). As our sample is relatively small, regional subdivision appeared unjustified.

The blood samples were air-mailed to Mainz, where all the laboratory tests were done, using the usual serological and biochemical

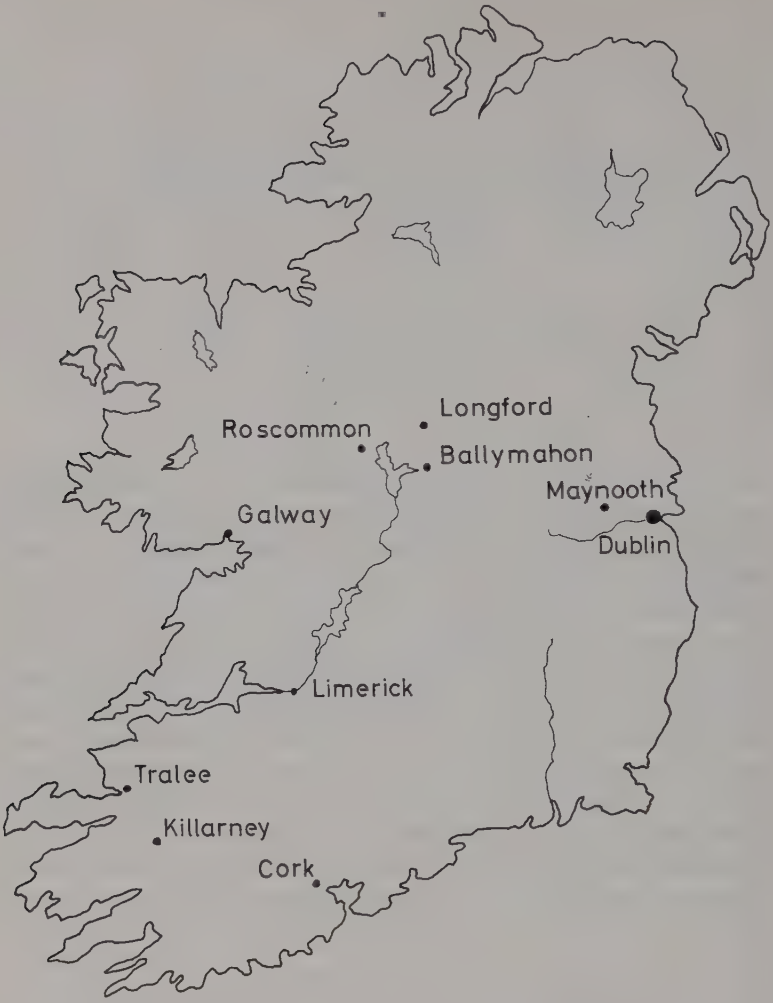

FIG. 1

methods as described by Boorman and Dodd (1970) and by Giblett (1969). In this way the following characters were examined: ABO, MNS, Rh, P, Kell, and Duffy (a) blood groups; haptoglobin, Gc, Gm (1, 2, 5), and Inv (1) groups; red cell acid phosphatase, adenylate kinase, phosphoglucomutase and serum alkaline phosphatase. The $beta_2$-glycoprotein I phenotypes were typed as described by Koppe *et al.* (1970); the technique of ceruloplasmin typing was as set out by Bajatzadeh and Walter (1969). For blood grouping we used reagents from the Ortho Pharmaceutical Corp., Raritan, N.J. (USA). Gc-, Gm- and Inv-typings were carried out using reagents produced by H. Molter Limited, Heidelberg (West Germany).

Results

(i) *Blood Groups.* The blood group results are set out in Table 1.

The ABO blood groups show good agreement between observed phenotype frequencies and those expected in Hardy Weinberg equilibrium (χ^2=0·21, 4 d.f., not significant). The gene frequencies are p_1=0·100, p_2=0·039, q=0·075, r=0·786.

TABLE 1. Blood groups

	Blood Group	Obs.		Exp. No.
		No.	%	
ABO	O	182	61·7	182·1
	A_1	50	17·0	51·6
	A_2	20	6·8	18·5
	B	37	12·5	36·4
	A_1B	6	2·0	4·6
	A_2B	—	—	1·8
		295	100·0	295·0
MNS	MS	85	28·8	78·2
	Ms	38	12·9	34·1
	MNS	58	19·7	72·0
	MNs	60	20·3	67·4
	NS	17	5·8	10·0
	Ns	37	12·5	33·3
		295	100·0	295·0
Rhesus	ccDE	56	18·9	50·1
	ccddee	52	17·6	47·7
	CcDee	81	27·5	98·0
	CcDE	31	10·5	36·9
	CCDee	54	18·3	43·0
	Ccddee	5	1·7	4·3
	ccDee	14	4·8	13·1
	ccddE	2	0·7	1·9
		295	100·0	295·0

In the MNS system, the observed and expected phenotype numbers, typed with anti-M, anti-N and anti-S sera, differ significantly ($\chi^2 = 9{\cdot}88$ 2 d.f. $P < 0{\cdot}01$). This may be a chance effect due to small sample size. The gene frequencies, calculated according to the formulae given by Schwarzfischer and Liebrich (1961), come to: $p^{MS} = 0{\cdot}277$, $p^{Ms} = 0{\cdot}340$, $p^{NS} = 0{\cdot}047$, $p^{Ns} = 0{\cdot}336$.

TABLE 2. Serum proteins

System		Obs. No.	Obs. %	Exp. No.
	Hp 1–1	44	14·9	42·2
Haptoglobin	2–1	135	45·8	138·7
	2–2	116	39·3	114·1
		295	100·0	295·0
Group specific component	Gc 1–1	166	56·3	168·2
	2–1	113	38·3	109·1
	2–2	16	5·4	17·7
		295	100·0	295·0
	Gm 1, −5, −2	19	6·5	13·5
	1, 5, −2	76	25·9	80·5
Gm groups	1, 5, 2	62	21·1	54·9
	1, −5, 2	18	6·0	24·6
	−1, 5, −2	119	40·5	120·5
		294	100·0	294·0

Similarly in the rhesus system there is some disagreement between the observed and expected phenotype numbers. We tested for the presence of antigens C, c, D, and E, and the expected values have been calculated as proposed by Balakrishnan (1962). The discrepancy especially concerns the phenotypes CcDee (in deficit) and CCDee (in surplus). This, however, may be due to small sample size, and too much stress should not be placed on the χ^2 value ($\chi^2 = 7{\cdot}95$, 2 d.f. $P < 0{\cdot}02$). The gene frequencies, calculated as proposed by Mourant (1954), are cde $= 0{\cdot}402$, Cde $= 0{\cdot}018$, cdE $= 0{\cdot}008$, cDe $= 0{\cdot}052$, CDe $= 0{\cdot}364$, cDE $= 0{\cdot}156$.

For the other blood groups, there are 133 (45·1 per cent) P positive individuals, and 162 (54·9 per cent) P negative; the frequency of the P-gene is 0·259. The number of Kell positive individuals is 17 (5·8 per cent) and of Kell negatives 278 (94·2 per cent); the gene frequency p^K is 0·029. Duffy positive (Fy a+) individuals numbered 152 (51·5 per cent), negative (Fy a−) 143 (48·5 per cent); the gene frequency Fy^a is 0·304.

(ii) *Serum proteins.* For the haptoglobin system (Table 2) there is good agreement between the observed and expected numbers of phenotypes ($\chi^2=0\cdot21$, 1 d.f., not significant). The gene frequencies are $Hp^1=0\cdot378$, $Hp^2=0\cdot622$. No haptoglobin variants were seen.

Similarly in the Gc-system the observed Gc phenotype numbers conformed closely with those expected (Table 2, $\chi^2=0\cdot33$, 1 d.f,. not significant). The gene frequencies are $Gc^1=0\cdot755$, $Gc^2=0\cdot245$.

The Gm-system also showed good agreement between observed and expected phenotype numbers (Table 2, $\chi^2=5\cdot20$, 2 d.f., not significant). The gene frequencies are $Gm^1=0\cdot214$, $Gm^{1,2}=0\cdot146$, $Gm^5=0\cdot640$.

In the Inv-series, 43 (14·6 per cent) of the subjects showed the phenotype Inv (1), whilst 251 were of phenotype Inv (−1).

TABLE 3. The beta$_2$-glycoprotein I-system and Ceruloplasmin system

		Obs.		Exp.
	System	No.	%	No.
beta$_2$-glycoprotein I	Bg N–N	96	89·7	96·2
	N–D	11	10·3	10·5
	D–D	—	—	0·3
		107	100·0	107·0
Ceruloplasmin	Cp A	—	—	0·02
	AB	6	2·5	4·74
	B	232	96·7	234·28
	AC	—	—	0·01
	BC	2	0·8	0·95
	C	—	—	<0·001
		240	100·0	240·00

The beta$_2$-glycoprotein I-system showed 10 per cent of heterozygotes, the observed and expected phenotype numbers (Table 3) showing no significant deviation ($\chi^2=0\cdot01$, 1 d.f., not significant). The gene frequencies are $Bg^N=0\cdot948$, $Bg^D=0\cdot052$.

Results for the ceruloplasmin system, also given in Table 3, similarly showed good agreement of observed and expected phenotype values ($\chi^2 = 0 \cdot 57$, 1 d.f., not significant). The gene frequencies are $Cp^A = 0 \cdot 012$, $Cp^B = 0 \cdot 983$, $Cp^C = 0 \cdot 004$.

(iii) *Isoenzymes.* The red cell enzyme results are shown in Table 4. For red cell acid phosphatase agreement between observed and expected phenotype numbers is not quite satisfactory ($\chi^2 = 9 \cdot 16$, 2 d.f., significant at 0·02). Discrepancies occur especially in phenotypes AcPh A and AcPh B (in surplus) and AcPh BA (in deficit). The gene frequencies are $p^A = 0 \cdot 288$, $p^B = 0 \cdot 676$, $p^C = 0 \cdot 036$.

TABLE 4. Red cell isoenzymes

	System	Obs. No.	%	Exp. No.
Acid phosphatase	AcPh A	35	11·9	24·5
	BA	95	32·2	115·0
	B	144	48·8	134·6
	CB	16	5·4	14·4
	CA	5	1·7	6·1
	C	—	—	0·4
		295	100·0	295·0
Adenylate Kinase	AK 1	92	80·7	86·9
	2–1	15	13·2	25·3
	2	7	6·1	1·8
		114	100·0	114·0
Phosphoglucomutases	PGM_1 1	82	77·4	79·2
	2–1	19	17·9	24·9
	2	5	4·7	1·9
		106	100·0	106·0

For adenylate kinase however observed and expected phenotype frequencies (Table 4) are in reasonable agreement ($\chi^2 = 1 \cdot 02$, 1 d.f not significant). The gene frequencies are $AK^1 = 0 \cdot 873$, $AK^2 = 0 \cdot 127$.

Similarly phosphoglucomutase types (Table 4) show no significant deviation of observed from expected phenotype numbers ($\chi^2 = 0 \cdot 26$, 1 d.f., not significant), though the slight excess of homozygotes is of interest. This may possibly be due to chance effects, as the actual number of tested individuals is small. But surpluses of PGM_1 1 and

PGM_1 2 homozygotes and deficits of PGM_1 2–1 heterozygotes have also been seen in other populations, e.g. Icelanders (Mourant and Tills, 1967), and Germans from southwest Germany (Wille *et al*,, 1968), and this phenomenon deserves further investigation to see whether it indeed has a biological basis. The gene frequencies in our Irish samples are: $PGM_1{}^1 = 0{\cdot}864$, $PGM_1{}^2 = 0{\cdot}136$.

The results for serum alkaline phosphatase are given in Table 5. The distribution of types Pp 1 (with one band) and Pp 2 (with two bands) is strongly associated with the ABO blood groups, the majority of types Pp 2 occurring with blood groups O and B. This association is highly significant ($\chi^2 = 15{\cdot}18$, 2 d.f., $P < 0{\cdot}001$). This agrees with similar observations on other populations (Chopra, in press, Walter 1968).

TABLE 5. Serum alkaline phosphatase types

Blood group	N	Pp 1	Pp 2
O	164	45 (27·3%)	119 (72·9%)
A	64	35 (54·7%)	29 (45·3%)
B	34	11 (32·5%)	23 (67·7%)
AB	6	2	4
	268	93 (34·7%)	175 (65·3%)

Discussion

Comparing phenotype and gene frequencies of our Irish sample with those available for other European populations, it can be seen that in the polymorphic systems MNS, Rh, Kell, haptoglobin, Gc, Gm, Inv, beta$_2$-glycoprotein I, ceruloplasmin, red cell acid phosphatase and adenylate kinase, no real differences between the Irish and other Europeans occur. On the other hand, more marked differences emerge regarding the following polymorphisms: ABO, P, Duffy, phosphoglucomutase and serum alkaline phosphatase.

The frequencies of p^P (0·259) and Fy^a (0·034) found in our Irish sample are somewhat lower than in other European samples. However, further research is needed to show whether this is a chance effect due to small sample size, or a characteristic of the Irish.

Relatively low frequencies as compared to other European populations are also present regarding the alleles A (0·139) and B (0·075) of the ABO system, whereas the O-allele (0·786) is at a much higher frequency than common for Europeans. This was demonstrated previously by Hackett (1956). It is of considerable interest that the ABO-distribution in Ireland is very similar to that of Iceland (Palsson and Walter 1967). This may reflect genetical relationship between these two populations, but may also be due to parallel selective processes, as suggested by Mourant (1954): "Similarity in gene frequencies may reflect convergence due to similar environments." In this connection the distribution of serum alkaline phosphatase is also of considerable interest, as demonstrated by Walter (1968) and more recently by Chopra (in the press). The frequency of the so-called Pp 2 alkaline phosphatase type shows a marked geographical pattern with highest frequencies in Iceland (64·4 per cent) and Ireland (65·3 per cent). However, as the genetical basis of the Pp 2 phenotype is still unclear, and as effects of diet, especially fat consumption, on the intestinal alkaline phosphatase of individuals of a particular genetic constitution (B and O secretors) have been established (Langman *et al.*, 1966), we do not know whether these similarities reflect genetical relations between Icelanders and Irish or whether they are due to similar dietary habits of both populations. Further research on the control mechanism of serum alkaline phosphatase is necessary in order to understand the significance of this similarity and the differences in the world distribution of phosphatase types.

The Irish differ from other European populations also in the frequencies of the PGM$_1$ alleles, since PGM$_1^1$ (0·864) has a higher frequency in the Irish and PGM$_1^2$ a lower. However, within Europe a clear distribution gradient is to be seen, with the PGM$_1^2$ frequencies increasing generally from north to south (Bhasin and Fuhrmann 1972). Irish (0·136), Icelanders (0·182, Mourant and Tills 1967), Danish (0·194, Lamm 1970), and Finland-Swedes (0·196, Eriksson *et al.* 1971) show the lowest frequencies of this gene out of all European populations so far tested except the Lapps, whereas in Germany (0·209–0·257), Austria (0·209), Czechoslovakia (0·219), Italy (0·238–0·296) and Greece (0·307) the frequencies are obviously higher. The biological significance of this distribution pattern is still unclear and requires further research.

Summary

The results of blood, serum and enzyme group typings on a sample of 295 unrelated Irish males aged from 20–30 are reported. The gene

frequencies concerning the polymorphic systems MNS, Rh, Kell, Hp, Gc, Gm, Inv, beta$_2$-glycoprotein I, ceruloplasmin, red cell acid phosphatase and adenylate kinase do not differ obviously from those of other European populations. On the other hand our Irish sample differs regarding the gene frequencies of the ABO, P, Duffy and PGM$_1$ polymorphisms and in the frequencies of the serum alkaline phosphatase phenotypes. Finally, the gene distribution of the Irish seems to be more similar to those of the Icelanders as compared to other European populations, which may reflect some genetical relationship between these two populations.

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GENETIC FACTORS IN THE ISLE OF MAN AND NEIGHBOURING AREAS

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THE genetic survey of the Isle of Man has two particular aims. The first is to compare the indigenous population of the island with other British populations especially those of Cumberland and southwest Scotland. These are nearest geographically to the Isle of Man and there has been a great deal of contact between them throughout the Island's history. The second aim is to determine whether any intra-island differences in the frequencies of genetic factors exist. Before this can be achieved each individual tested has to be allocated to a geographical division of the island on the basis of his or her ancestry. This stage of the analysis is not yet complete.

What constitutes a native Manx individual? The criterion used is that both parents and at least three grandparents of each individual incorporated in the survey were born on the Isle of Man. This restricts the number one is able to test, but it was felt that only in this way could a truly Manx sample be acquired, one which allows comparison of the findings of this survey with previous studies of the Island's population.

The first descriptive study was carried out by Beddoe in 1887 when he recorded the measurements of the heads of 31 Manxmen and observed the colours of the eyes and hair of 265 others. A. W. Moore in conjunction with Beddoe carried out the next research in 1898, an analysis of the recorded physical attributes of recruits of the Royal Manx Fencibles, a militia formed on the Island during the Napoleonic Wars.

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The end product of the Island's history, that the population is by no means uniform in its physical characteristics, was first demonstrated at that time, and again later in greater detail by Davies and Fleure in 1936. After analysis of various measurements of 1200 Manxmen who had four grandparents born on the Island and whose surname was present on the Island before 1700, they concluded that two "physical types" were predominant on the Island, the "Medi-

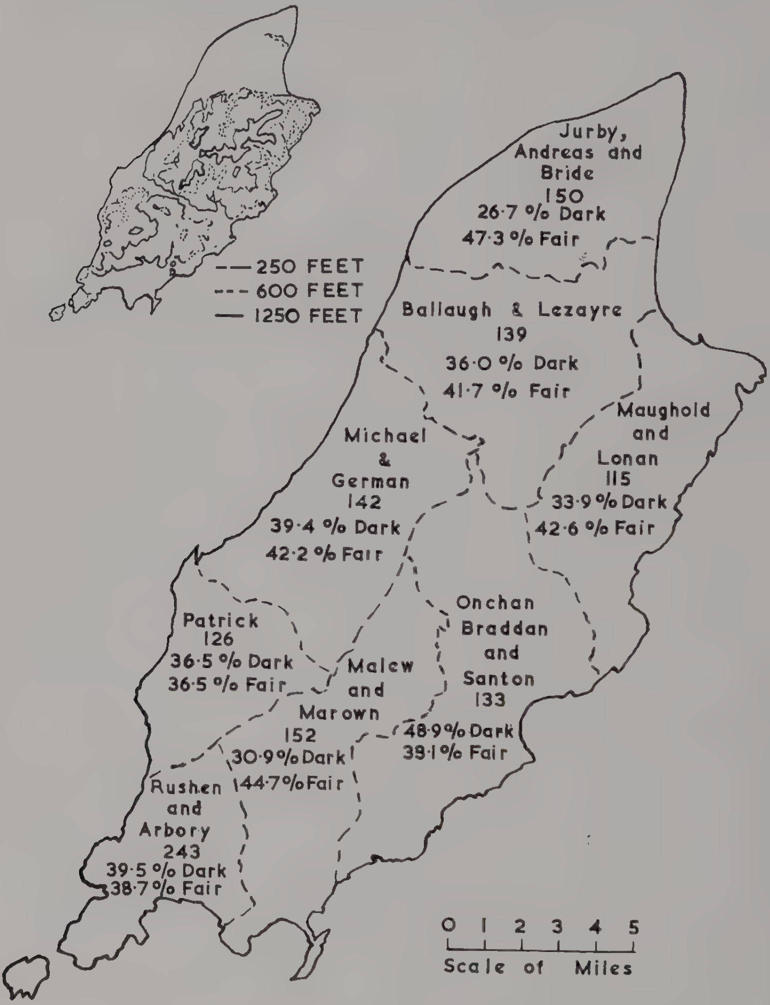

FIG. 1

terranean" and the "Nordic". According to Davies and Fleure, individuals combining dark brown or black hair, with brown eyes, long narrow heads and medium stature are most numerous in the parishes of Onchan, Braddan and Santon (Figure 1). Those distinguished by fair hair, light eyes and taller stature are said to be most frequent in the north, especially in the parishes of Bride, Andreas and Jurby, as well as in Malew in the southeast.

In the present survey the genetic factors investigated include most of the blood group antigens, the serum proteins haptoglobin and transferrin, and the red blood cell isoenzymes including acid phosphatase. Non-serological data collected include phenylthiocarbamide (P.T.C.) taste sensitivity, palm and finger prints and skin colour measurements.

Results

Table 1 shows the distribution of the ABO groups within three separate series of Manx individuals. These three samples comprise adults who are not blood donors, secondary schoolchildren and blood donors respectively. The most interesting feature of the Table is that the blood donors differ in the frequencies of O and A from the other two series (A = 36 per cent compared with 47 per cent and 49 per cent; O = 54·6 compared with 43 per cent and 40 per cent; ratio A/A+O 39·8, 52·0, and 55·0). The adult non-donors and the schoolchildren could be grouped together in one sample, as there was no significant difference between them. This was done, and a χ^2 test performed on the frequency of O between the two remaining

TABLE 1. ABO blood groups—Isle of Man

Phenotype	Adults		Schoolchildren		Blood donors		Total	
	n	%	*n*	%	*n*	%	*n*	%
A	49	49·0	159	47·0	78	36·1	286	43·7
B	7	7·0	24	7·1	12	5·6	43	6·6
AB	4	4·0	9	2·7	8	3·7	21	3·2
O	40	40·0	146	43·2	118	54·6	304	46·5
Total	100	$\frac{A}{A+O}=55\cdot1$	338	$\frac{A}{A+O}=52\cdot1$	216	$\frac{A}{A+O}=39\cdot8$	654	$\frac{A}{A+O}=48\cdot5$

2×2 χ^2 Test; Adults + Schoolchildren v. Blood Donors;
O v. non O = 8·1; significant at the 1 per cent level.

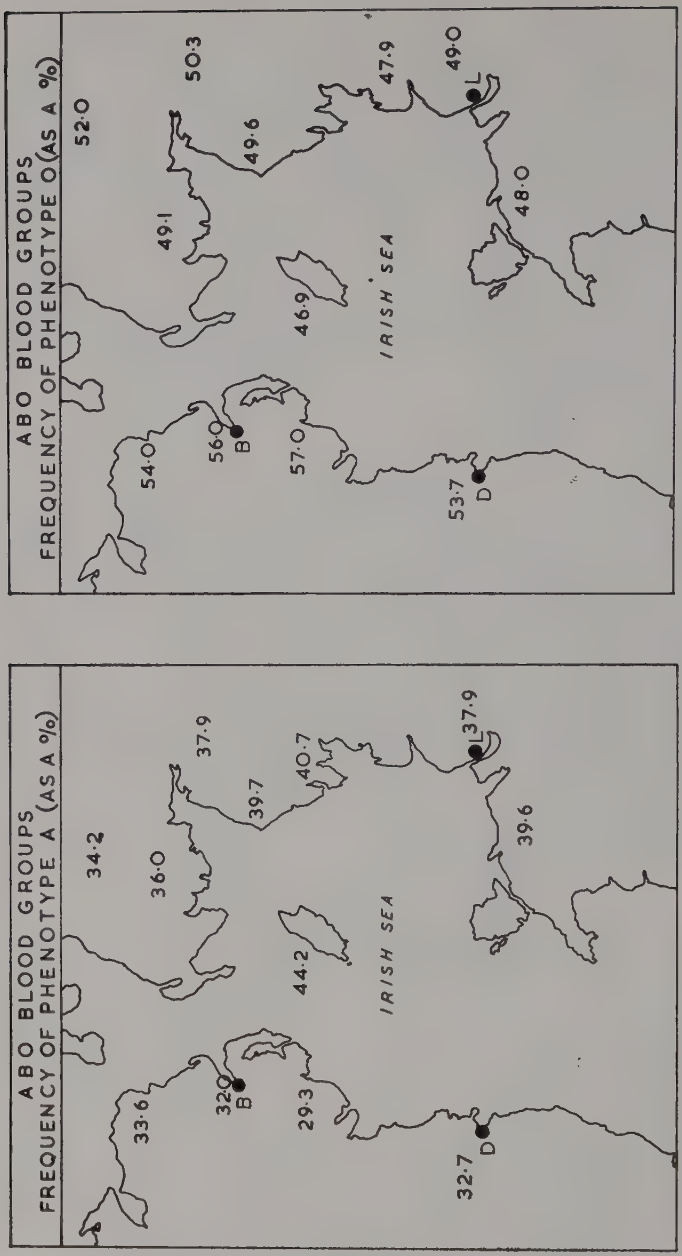
ABO BLOOD GROUPS
FREQUENCY OF PHENOTYPE O (AS A %)
52·0
50·3
49·1
49·6
47·9
49·0
L
48·0
46·9
IRISH SEA
54·0
56·0
B
57·0
53·7
D
ABO BLOOD GROUPS
FREQUENCY OF PHENOTYPE A (AS A %)
34·2
36·0
37·9
39·7
40·7
37·9
L
39·6
44·2
IRISH SEA
33·6
32·0
B
29·3
32·7
D

FIG. 2

samples; blood donors versus schoolchildren and adults. The differences between these two series is highly significant, yet they are equally Manx by ancestry.

A possible reason for this disparity between the samples may be that the Blood Transfusion Service on the Island recalls donors to bleeding sessions on a selective basis and hence there may be a bias towards O blood. More important perhaps, is the consideration that because those individuals requiring blood transfusions and blood products are drawn at random from the total population of the Island, it may be that the frequency of the ABO groups amongst indigenous Manx donors (39 per cent A) reflects more accurately the frequency of ABO groups to be found in the general population of the Isle of Man, that is those with and without Manx ancestry.

Another possible explanation for the difference between the three series was suggested by Kopeć (1970) in a different context, for the Isle of Man was one of the few areas not covered by her research. She believes her blood donor samples to be representative of the populations of which they are a part. However she adds that "even in proportion to their total number, rural populations are likely to be less well represented among donors than the inhabitants of towns. It may happen that some important rural groups have been missed or represented so sparingly as to be swamped statistically by their urban neighbours." The majority of bleeding sessions in the Isle of Man are held in Douglas, the urban centre, and as a result the majority of donors reside there. However the schoolchildren sample includes all indigenous Manx children between the ages of 11 and 16 who wished to take part in the survey (and there were few refusals). This meant that the catchment area of the schools encompassed the whole island.

Figure 2 shows the distribution of phenotypes O and A in the Isle of Man and neighbouring areas. The figures for the mainland are compiled from frequencies given by Kopeć, and her allocation of individuals to specific areas is on the basis of postal address. The figures for the Isle of Man represent the amalgamation of all individuals tested. If the Manx donors are taken as representative (54 per cent group O) of the Island's population, then the ABO distribution fits in well with the pattern found in the Irish Sea area. However if the non-donor groups are taken as representative (43 per cent group O) then the Isle of Man stands out as being significantly different from the surrounding populations.

There is interesting independent support for this difference. When a survey of indigenous secondary schoolchildren in Cumbria was undertaken, the ABO frequencies were found to differ from those given by Kopeć 1970 for blood donors in the same area. All the schoolchildren tested had three or more grandparents born in the area known as Cumbria, whereas the donors' only qualification was residence. The frequencies of the ABO phenotypes in 341 secondary schoolchildren of both sexes are given in Table 2, as are the frequencies for Northern Region 3 of Kopeć, which comprises the counties of Cumberland, Westmorland, West Durham and northwest Yorkshire. Though there was found to be no statistically significant difference between these two samples for the ABO groups tested overall ($\chi^2=6\cdot1$, 3 d.f.), comparison of O versus not-O was significant at the 5 per cent level ($\chi^2=4\cdot9$, 1 d.f.).

TABLE 2. ABO Blood groups

Phenotype	"Native" Cumberland schoolchildren		Blood donors Kopeć Region 3	
	n	%	*n*	%
A	156	45·75	7,943	39·84
B	30	8·80	1,594	8·00
AB	8	2·35	566	2·84
O	147	43·10	9,834	49·32
Total	341	$\frac{A}{A+O}=51\cdot5$	19,937	$\frac{A}{A+O}=44\cdot7$

2×2 χ^2 Test; Cumberland Schoolchildren v. Blood Donors;
O v. non O=4·9 $p<0\cdot05$

When the two samples of schoolchildren are compared for the frequency of ABO groups, it is seen that the distribution of the phenotypes in the two series is very similar (Table 3), the overall χ^2 value being 0·74, 3 d.f., and for A versus not-A 0·07, 1 d.f., neither being significant.

One conclusion that may be drawn from these tables is that when one investigates the population of any one geographical area however small, one should not assume that its population is homogeneous in its physical and genetic characteristics. It is possible that the physical attributes of the native or indigenous population may be swamped or at least greatly diluted by the resident, immigrant community. (This could apply to modern civilized populations like our own as much as to other groups.)

TABLE 3. ABO blood groups

Phenotype	Cumberland schoolchildren		Manx schoolchildren	
	n	%	n	%
A	156	45·75	159	47·0
B	30	8·80	24	7·1
AB	8	2·35	9	2·7
O	147	43·10	146	43·2
Total	341	$\frac{A}{A+O}=51{\cdot}5$	338	$\frac{A}{A+O}=52{\cdot}1$

$2\times 2\ \chi^2$ Test; Cumberland v. Manx schoolchildren
A v. non A $=0{\cdot}07$ $p=0{\cdot}80$

Figure 3 shows the frequency of the haptoglobin gene Hp^1 in a sample of 374 Manx as well as in neighbouring populations. The

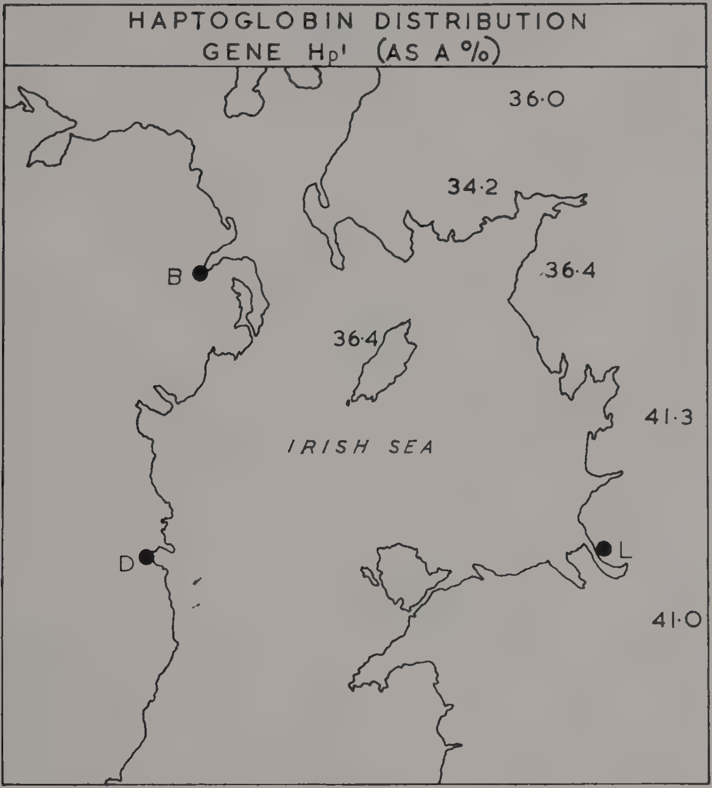

FIG. 3

frequency of gene Hp^1 is identical with that found in Cumbrians and very similar to that found in southwest Scotland. Transferrin is another plasma protein which exhibits detectable inherited variants. Of 374 Manx specimens analysed, 8 variants of the faster moving BC type and 1 slower moving CD type have been found.

The red blood cell isoenzyme showing a valuable polymorphism is acid phosphatase which is controlled by three alleles, termed P^a, P^b and P^c. The number of the 6 phenotypes and the frequency of the three genes as a percentage are shown in Table 4. Again overall there is no significant difference ($\chi^2 = 11{\cdot}0$, 6 d.f.) but the CA+CB+C phenotype numbers are significantly different when the Isle of Man is compared with a series of students from northern England ($\chi^2 = 6{\cdot}0$, 1 d.f.).

TABLE 4. Acid phosphatase

Area	Total	Phenotype						Gene		
		A	BA	B	CA	CB	C	P^a	P^b	P^c
Isle of Man	345	45	132	126	15	26	1	34·4	59·4	6·2
Northern England	280	44	107	112	4	13	—	35·5	61·4	3·0
England	139	14	64	48	5	8	—	34·9	60·4	4·7

2×2 χ^2 Test; Isle of Man v. Northern England;
CA, CB, C v. rest = 6·0—significant at the 2% level.

As regards non-serological genetic variability Figure 4 shows the distribution of non-tasters of phenylthiocarbamide (P.T.C.) in populations surrounding the Irish Sea. All the figures relate to individuals whose parents and many of whose grandparents were born in the areas specified. The tasting procedure was modified from that of Harris and Kalmus (1949) in that only eight solutions were used. The antimodal value for all samples was taken at solution 4 in order to facilitate comparison. The difference in the frequency of non-tasters between the Isle of Man and North Wales is significant.

This survey of genetic factors in the Manx population has uncovered some interesting problems. One of these is the probable existence of a number of different genetically endowed populations on the Island. The suggestion appears to be that Manx native donors are distinct from other groups on the Island, especially indigenous schoolchildren in the frequency of ABO blood groups, yet the frequencies within the former group fit very well with the distributions found in other populations surrounding the Irish Sea.

There is no statistically significant difference between the indigenous schoolchildren populations of the Isle of Man and Cumberland for any of the genetic factors investigated.

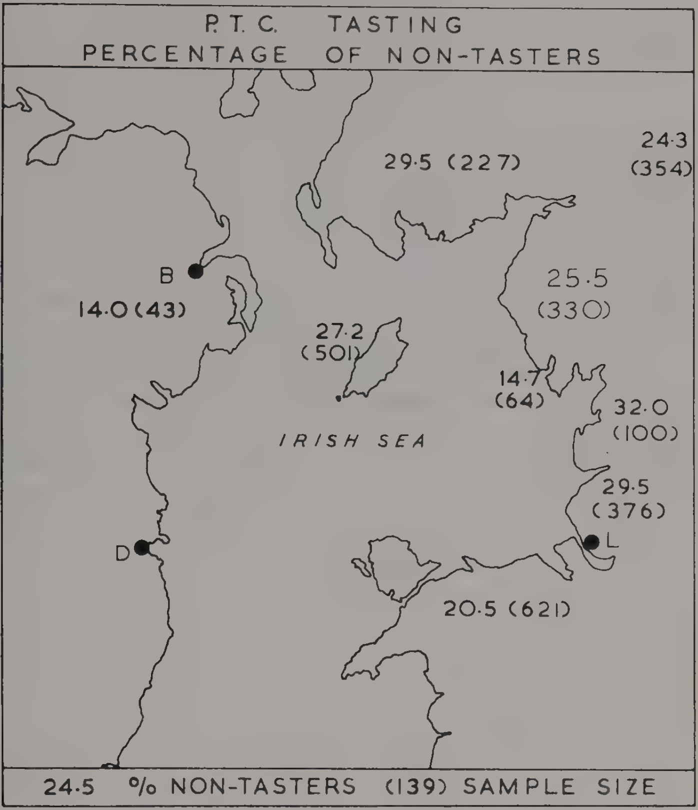

FIG. 4

Acknowledgements

In particular thanks are due to Dr. C. G. Pantin, Director of the Blood Transfusion Service on the Isle of Man, for his supervision of the collection and posting of blood samples to Durham. Also the survey would have been impossible without the cooperation of the Directors of Education of the Isle of Man, the City of Carlisle, and Cumberland as well as the Head Teachers of the various schools visited. Thanks are also due to Dr. S. Murray, Director of the Regional Blood Transfusion Centre in Newcastle, and Dr. J. Wallace, Director of the Glasgow and West of Scotland Blood Transfusion Service, for allowing blood specimens from their donors to be used in this survey.

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GENETIC FACTORS IN SOME BRITISH GYPSIES

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The fundamental question in this Gypsy investigation was that of which criteria could effectively be used in defining a Gypsy. There are, I am sure, many Romany-speaking itinerants, or to be more correct, persons who utilize Romany words as a second or secret language who are not of gypsy parentage, and equally, sedentary people who can lay claim to the "darkest" Romany lineage who for various reasons do not speak the language or, indeed, admit their heritage.

The appellation "Gypsy" is in itself misleading as it derives from the misnomer Egyptians (syn. Gipcy, Gipsyan.) given to the swarthy gaily-attired wanderers who appeared in Britain in the late fifteenth or early sixteenth century; the nomenclature of the travelling people who we have come to term gypsies also varies from country to country. To avoid confusion through inaccurate terminology (and, indeed from an ethnological point of view) it would be more correct to refer to them generally as itinerants or travellers, reserving the specific term for proven cases. Tradition states that they call themselves Zingary or Romany Chals. Zingaro is of Sanskrit origin signifying a man of mixed race whilst Chal is a Zingaric word denoting a son or lad—also a contraction of Chaval which is still used with the same meaning in Spain by the gypsies and peasants. The literal translation as "sons of Rome" seems more likely to derive from association with Rum, the territory of the Seljuk Turks, or Rama the Indian diety, rather than the Roman capital.

The word tinker is often erroneously applied to gypsies since their mode of life has resulted in many outward similarities to the travelling tinkers. The ethnic origins of the latter are different, though there is no definite proof as to their identity, but many authorities consider them to be of old Celtish stock, perhaps an occupational group, since the name describes the sound made in repairing pots and pans. Certainly there has been admixture with the gypsies to some degree but the expression "tinkler-gypsy" peculiar to Scotland is not necessarily proof of this. The British gypsies are however emphatic as to their differing lineage.

The itinerants of presumed Asian origin whom we know as gypsies or romanies are also variously referred to as Bohemians, Tziganes and Gitanes (France), Tartar or Tartare (Sweden), Heiden (Holland) and Zigeuner (Germany). The term Bemishe is probably analogous to Tinker, Fant (Finland), Vandrevolk (Denmark) and Gitano (Spain). These various national groups share a common tongue, Romanes, modified and utilized to a greater or lesser degree with indigenous languages. In general they are considered to be of small to medium stature, dark-eyed, of swarthy complexion and with black luxuriant hair, but their features have doubtless also been influenced by admixture with non-gypsy populations.

Gypsy subgroups

The expressions "posh-rat" and "didikais" rigorously defended by some authors as defining Romanichels of half-blood and less than half-blood status, appear to be in indiscriminate use. Clebert (1963) describes the gypsies in Europe as composed of three main groups:

(a) Kalderash, being tinsmiths, coppersmiths, smiths, etc. (word root derived from "caldera", a pot or cauldron)
(b) Manush, reputed Sanskrit origin as "true men" or Sinto.
(c) Gitanos, as the Spanish gypsy or "gitan".

None of the families or individuals met in this survey owned to such tribal or group allegiance. A volunteer social worker reported the presence of a larger Kalderash group assembled in England from smaller numbers entering the country through normal entry ports from the Continent, but I have been unable to substantiate this statement. One typically dark-eyed gypsy described her grandfather as Spanish; two others recalled Hungarian ancestry.

It is well acknowedged that many travelling families in the British Isles are not of Romany heritage and their status has been brought about by economic depression, war or other disaster. The first two Scottish travellers tested were sisters located in Essex with their

English (traveller) husbands at the time of testing; they had been born in tents in the Hebrides and by appearance could not be distinguished from the majority of travellers on the road today, but questioning drew out the dating of their family's itinerancy to the massacre of Glencoe. Similarly, a proud Scottish gipsy, leading the campaign for established caravan and camping sites for the travellers in Scotland, emphatically states that the true Scottish gipsy is not of Roman origin, distinguishing between such families and those having admixture with English gypsies, and also, with some disdain, the fairground travellers. The probability that these, together with the Irish travellers, are mostly of old Celtic stock with English admixture is high. The Romany language is in use with both groups, but Shelta or cant, as an abridged Gaelic dialect is frequently utilized.

Of interest also are the Northern or "Yorkshire" gypsies with traditions and history of travelling akin to the Romany, who recognize them as true gypsies, though not of Romany origin. As with the non-gypsy wanderers of central Europe who were at their zenith at the time of the Hundred Years' War (1338–1453), even forming their own Beggars' Guild, their origin is obscure, but they are probably derived from indigenous stock who took to the travelling life following socio-economic or political crises. Certainly such transition was easily achieved when we consider the contact, up to the early twentieth century, of villagers and people from towns less densely populated than now with the exotic gypsies at the then more important social gatherings of village fairs. An encounter with a family in York with at least four generations in transport and haulage brought out tales of stopping overnight at gypsy camp fires for company and using their horses to supplement the carters' animals on difficult ascents whilst traversing Northern England from coast to coast. At the few remaining fair gatherings, notably Appleby, the ruddy-faced Northern traveller mixes freely with those of Romany ancestry, often after travelling two or three days with a pony and cart used in his local hawking business to reach there. A basic interest in horses is apparent among travellers, away from cities whatever their ethnic origin.

The largest groups of travellers actually moving about together appear to be the Irish, both tinker stock or otherwise. The large groups hold together as a defensive measure and provide a substantial labour force and members do not seem to have hereditary group allegiance. Another large group of some 30 resplendent modern caravans wintering together was composed of Lees and Hernes (Herons) deriving from Wales with one middle-aged man acting as spokesman and leader. No information as to the size or number of family groups which moved together was forthcoming. While engaged in casual trading during the winter "stop-over" they described themselves as "showpeople" waiting for the summer fairs to commence.

The true British gypsies or Romanichels are very different in innumerable ways from other itinerants but many of these are intangible characteristics difficult to define. They are further quoted as being on the whole peaceable people, seldom making nuisances of themselves, probably following in a less intensive way the traditions observed by gypsies on the continent, but they do not approach continental gypsies as either dancers or musicians and are not as blazingly colourful as some continentals. In his comprehensive study based on material from the Journals of the Gypsy Lore Society, Van Wyk, however, noted several points of social resemblance between gypsies of the S.E. Balkans, Germany and England.

Present Status

In 1965 a census of travellers "on the road" in England and Wales was organized by the Ministry of Housing and Local Government with a view to resolving their social problems. The number in those areas was given as 15,000. The compilers considered this to be an underestimation of their true number, however, and a noted member of the Gypsy Lore Society offers an estimate of 50,000 "gypsies" in the British Isles, sub-divided thus:

(1) Romanies, about 10,000—"true" Romanichels.
(2) Posh-rats, about 10,000—half bloods.
(3) Didikais, about 10,000—less than half-blood.
(4) Travellers, about 20,000—no Romany blood.

The two totals may not be strictly comparable as Scotland and Ireland are not accounted for in the Ministry survey, but it seems doubtful that these two regions would account for such a large discrepancy so that the true numbers may perhaps be considered to lie between these two estimates. Certainly I also met a number of "settled" gypsies with considerable Romany ancestry, who in not presenting housing problems would have been omitted from the official census.

Whilst there is an increasing trend to become sedentary resulting from the main pressures of obtaining education for the children and diminishing camping sites under modern traffic conditions etc., it is probable that the greater proportion of British gypsies is still travelling the roads in the warmer months with, perhaps a static winter period.

It would be difficult but not impossible, at least back to the early nineteen century, to assess the degree of consanguinity in the British, and particularly the English, gypsies, as there can be no doubt that endogamy was and is practised among them, albeit with waning incidence as a result of education and increasing social contact with non-gypsy potential marriage partners. In agreement with their professed Indian ancestry, the absence of formal betrothal and bride-price with some-time elopement, frequent retention of maiden name on marriage and the esteemed position of the wife in the English gypsy family are all indications of a mother-right society. Whilst kinship is now recognized through both parental lines, there are firm indications that matriliny and matrilocality have been superseded at a comparatively recent date.

The Survey

There are no studies of the genetics of British gypsies. The intention of this survey was to examine a number of simply inherited characters, and to establish the gene frequencies, in order to make comparisons among gypsy subgroups, with British non-gypsy populations and with gypsy peoples elsewhere. It was hoped to obtain blood specimens, saliva and urine samples from at least one hundred (ostensible) Romanichels, carry out colour vision and other tests, and collect anthropometric and skin pigmentation measurements. The work was carried out under the auspices of the Department of Anthropology at Durham University, in cooperation with the Medical Research Council Serological Population Genetics Unit, London. It commenced in October 1968 but was suspended for financial reasons early in 1970.

Quite early in the project it became apparent that special problems faced the investigator, not only in classifying and making initial contact with the subjects, but in explaining the purpose of the research. Many of the often illiterate travellers are highly intelligent persons of widely acquired knowledge—television and radio have opened up new fields for discourse—and tactful and detailed explanation is required. Many of the families travelling our roads have been subjected to ill treatment by various individuals in both private and official capacities, and resentment of the gorgio or non-gypsy is inevitable. Group authority or even familial dominance does not appear to be valid within the present social structure so that lengthy explanations were required in virtually each family and sometimes with individual members of the unit, often with negative end result!

The first contacts with Britain's travelling folk were made through the Gypsy Council to which we had been referred by the Ministry of Housing and Local Government. It was later established that the Council's avowed function of resolving the social problems of travellers without distinction as to ethnic origin had resulted in hostility between leading English gypsies and the Council and this added to the difficulties for the research programme. We proceeded slowly from contact to contact. The summer fair gatherings appeared to offer opportunity for enhanced collection, but in practice proved disappointing as the travellers resented the intrusion of a gorgio in such capacity at functions which they regard as exclusively for the gypsy. This attitude was explained by a gypsy of well authenticated lineage who, having refused tests at one of the fairs, co-operated in full in the privacy of his home.

The gypsies generally exhibited deep-seated fear of blood sampling. Whilst the project was directed at an analysis of genetic factors, some return to the travellers was made by examination of the haemoglobin levels and packed cell volumes of the blood samples together with simple screening tests of urine specimens for abnormalities. The co-operation of local health officials was sought in all aspects of the survey and any abnormal findings refered to them. On one site where a severely anaemic boy was detected (who was also deaf and colour-blind) far greater response in the general tests was apparent on the next visit. It was of interest that the Romanies, often with a dread of ill-health being detected, displayed far more interest in the genetic inference whilst the Irish travellers were concerned with health aspects.

During the eighteen months of the survey, approximately 250 blood specimens were collected from itinerants in various parts of

England, and these were tested in eleven different blood group systems, eight enzyme systems, haptoglobin, transferrin and abnormal haemoglobin types. On rather fewer subjects tests for colour vision defects, tasting threshold and secretor status were also effected. The subjects were classified, utilizing a questionnaire as to familial history (cross-checked with other travellers as frequently as possible) and physical appearance, into one of five arbitrary groups, (a) those having some Romany lineage, and (b–e) those non-Romany (including doubtful cases) itinerants according to the four geographical areas of origin in England, Scotland, Wales and Ireland. The results now reported concern those subjects of Romany lineage, of whom there are 109.

Results

The results are given in Tables 1–6, where they are compared with those from other recent gypsy studies. Until 1951 there had been eleven serological studies on the ABO groups of Gypsy communities in Hungary, Rumania, Yugoslavia and Uzbekistan, whilst in that year Cazal *et al.* carried out research on French Gypsies at Perpignan, Montpellier and Saint Maries-de-la-Mer, which included differentiation of the A_1/A_2 sub groups together with MN and Rhesus grouping. In these series all observers agreed that the Gypsies have about 20 per cent A genes together with B gene frequencies well above European levels (Yugoslavia 21 per cent, Hungary 25 per cent, France 31 per cent). The frequencies of Rhesus negatives were 12·7 per cent in Hungary and 14·1 per cent in France where the main difference from most European populations is the high frequency of R_1 and low level of R_2. In the French study the M gene frequency reaches the rather high level of 59·3 per cent. The ABO frequencies of these studies strongly support the theory of North Indian origin, whilst their Rhesus and MN frequencies, though not differing as much as might be expected from European values, are also consistent with it.

The Swedish survey of Dr. Beckman (1965) on 115 travellers from the Stockholm area was, however, greatly at variance with the earlier studies. From an estimated Gypsy population of 900 (in Sweden), of which 300 were around Stockholm, he eliminated from his sample mixed Swedish-Gypsy offspring, also occasional Spanish and Finnish Gypsies. Beckman reports that "In the Rhesus, MN

TABLE 1. ABO blood groups in gypsy studies—1951 and after

		Phenotype								Gene frequency			
		A_1	A_2	B	A_1B	A_2B	O	χ^2	Total	p_1	p_2	q	r
French gypsies (Cazal *et al.* 1951)	No.	26	3	43	11	5	25	2·20	113	0·1942	0·0275	0·3064	0·4719
	%	23	2·7	38·1	9·7	4·4	22·1						
Slovenian gypsies (Avćin *et al.* 1961)	No.	117	56	36	13	8	120		350	0·2065	0·1240	0·0823	0·5873
	%	33·42	16·0	10·28	3·71	2·28	34·28						
Swedish gypsies (Beckman *et al.* 1965)	No.	55	13	7	3	1	36	1·20	115	0·2976	0·0929	0·0519	0·5583
	%	47·8	11·3	6·1	2·6	0·9	31·3						
British gypsies (Present Investigation)	No.	36	16	9	5	0	43		109	0·2004	0·1093	0·0636	0·6268
	%	33·03	14·68	8·26	4·58	0	39·45						

TABLE 2. MN blood groups in gypsy studies—1951 and after

		Phenotype					Gene frequency	
		MM	MN	NN	χ^2	Total	M	N
French gypsies	No.	31	40	15	0·11	86		
(Cazal *et al.* 1951)	%	36·05	46·51	17·44			0·5930	0·4070
Slovenian gypsies	No.	67	164	119	3·04	350		
(Avćin *et al.* 1961)	%	19·14	46·86	34·00			0·4257	0·5743
Swedish gypsies	No.	23	64	28	1·52	115		
(Beckman *et al.* 1965)	%	20·0	55·7	24·3			0·4785	0·5215
British gypsies	No.	54	45	10	0·02	109		
(Present Investigation)	%	49·54	41·28	9·17			0·7018	0·2981

TABLE 3. Rhesus blood groups in gypsy studies—1951 and after

		Phenotype								Chromosome frequency*						
		CDee	CDE	ccDE	ccDee	Cddee	ccddE	ccddee	No.	CDE	CDe	Cde	cDE	cdE	cDe	cde
French gypsies (Casal *et al.* 1951)	%	76·64	3·74	0·93	3·74	1·87	0	13·08	107		0·5496	0·0255	0·0235		0·0474	0·3540
Slovenian gypsies (Avčin *et al.* 1961)	%	61·51	12·28	7·41	0	4·57	0	14·28	350	0·0028	0·4431	0·0564	0·1209			0·3768
Swedish gypsies (Beckman *et al.* 1965)	%	76·52	13·04	6·09	0	0·87	0	3·48	115		0·6844	0·0261	0·1029			0·1906
British gypsies (Present Investigation)	%	55·96	19·27	10·09	0	0·91	0·91	12·84	109		0·4894	0·0133	0·1489	0·0133		0·3348

*Frequencies recalculated.

and haptoglobin groups there are significant differences between the Swedish Gypsies and the Swedes, but in addition there are significant differences between the Swedish Gypsies and other groups of European Gypsies concerning the A_1A_2BO and MN groups". These differences from other European Gypsies lay in a low proportion of Group B (6 per cent as compared with 38 per cent in the French series) and a high frequency of group A of 59 per cent of which 11 per cent were of sub-type A_2. In the MN system the M gene frequency (at 48 per cent) was lower than Cazal's French Gypsies—and, in fact, also than the local Swedish population. Beckman attributed such differences to genetic drift within a social isolate.

TABLE 4. Various blood group systems

Ss			
	S+	S−	Total
No.	45	64	109
%	41·28	58·72	
Lutheran			
	$\mathrm{Lu^a}$+	$\mathrm{Lu^a}$−	Total
No.	5	102	107
%	4·67	95·33	
Lewis			
	$\mathrm{Le^a}$+	$\mathrm{Le^a}$−	Total
No.	10	99	109
%	9·17	90·83	
Duffy			
	$\mathrm{Fy^a}$+	$\mathrm{Fy^a}$−	Total
No.	63	43	106
%	59·43	40·57	
Kell			
	K+	K−	Total
No.	5	103	108
%	4·63	95·37	

All subjects were also tested for the following systems, and all were negative: Hunter, Henshaw, Verwoerst, Wright, Diego

Our own findings in the A_1A_2BO groupings tend toward the Swedish Gypsy figures rather than the earlier results of high Group B frequency. Of critical importance therefore is Avcin's (1969) work on

TABLE 5. Haptoglobin and transferrin types

		Haptoglobin type					Transferrin type		
		1	2–1	2	χ^2	Total	Tf C.	Tf B–C	Total
Swedish gypsies (Beckman *et al.* 1965)	No.	0	27	88	1·25	115	115	Nil	115
	%	0	23·5	76·5			100		
British gypsies (Present investigation)	No.	16	54	33	0·35	103	100	3	103
	%	15·5	52·4	32·0			97·1	2·9	

	Gene frequency	
	Hp 1	Hp 2
Swedish gypsies (Beckman *et al.* 1965)	0·117	0·883
British gypsies (Present Investigation)	0·417	0·583

350 Gypsies in Slovenia carried out in 1961, which shows a very low B gene frequency (8·78), high A_2 frequency (12·50), very low M frequency (42·57), a low percentage of non-secretors (10·90) and imposing differences in frequencies of Rhesus combinations compared with the surrounding indigenous Slovenes. Beckman was presumably unaware of Acvin's work of 1961 as no reference was made to it in his publication, and his comment as to the possible influence of genetic drift in the Swedish group, whilst reasonable in the original text, is less so in the light of the comparative findings on the large numbers of Slovenian Gypsies.

TABLE 6. British gypsies, other tests

Secretor status (ABH)			
	Secretor	Non-secretor	Total
No.	48	9	57
%	84·2	15·8	
Tasting			
	Taster	Non-taster	Total
No.	25	10	35
%	71·4	28·6	
Colour vision			
	Normal	Red/green deficiency	
No.	57	1	
%	98·3	2·0	
		Total colour blindness	Total
No.		1*	59

* Non-gypsy mother

Our own data are in close agreement with the latter studies with low Group B and raised A_2 levels but the M gene frequency is of Indian magnitude at 70 per cent, but the haptoglobin types are not in accord with the dramatic low level of Hp1 shown in the Swedish study. An interesting finding is the number of transferrin variants, detected in the British Gypsies. These are being further analysed, for their amino-acid pattern may offer further indication of their "ethnic origin".

These similarities and differences are of interest in relation to nomenclature and locational distribution of modern European

Gypsy groups. Dr. Kenrick recently kindly suggested a division on the basis of the names by which they term themselves:

(1) Kalo	Finland, Spain, Wales
(2) Śinto	Sinto and Manouche nomads
(3) Rom	All the others (including English Gypsies, Slovenian and Kalderash)

If it is accepted that the French investigations apply to Group 2 and the others to Group 3, our results suggest some genetic basis for the subdivision of European Gypsies by linguistic criteria, and are most encouraging for further research into their physical anthropology.

Conclusion

At this intermediate stage of the investigation I am dissatisfied at the deficiencies in various sections and at my inability to offer explanation of the results so far. As with all such investigations our scant knowledge of natural selective forces and gene association is, once again, emphasized and I am loth to offer an opinion as to the antecedents of the group of British Gypsies examined. On serological evidence I would suggest that, however united their brotherhood, our European Gypsies have at least two ethnic origins and that in these enlightened days of racial admixture there is an urgent case for further research into the human biology of the present day groups.

At present there are proposals to study Welsh Gypsies and to remedy the deficiencies in testing on the other groups of British travellers. On a longer term I should like to see investigations in Turkey and the North African South Spanish littoral to obtain base-line gene frequencies of the various factors at these "land bridges".

The difficulties of obtaining adequate finance for such work are accompanied by those of finding the right type of researchers, able to work among a suspicious but nevertheless warm, friendly people who have been denied many of the social advantages of conventional house-dwellers.

Acknowledgement

It is very easy to state methodically acknowledgements to this person and that; how much more difficult to express my debt of gratitude to the many persons who each contributed to this study.

To my travelling friends who put up with needles and spitting into bottles, to the health officials, municipal and social workers who suffered my intrusion into their daily work, to Dr. A. E. Mourant as my Director and counsellor of longstanding, and to his staff who laboured on the enzymes and to my friend, Professor E. Sunderland, who extended the hospitality of his Department.

On the practical side, I am indebted to Dr. K. Goldsmith and Dr. N. Shephard for supplies of antisera, and grateful for the financial assistance of the Horniman Trust and, indirectly through Professor Sunderland, the Eugenics Society.

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THE Gm(1) AND Gm(2) FACTORS IN SCOTLAND

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A PRELIMINARY study of the distribution in Scotland of the serum immunoglobulin allotype, Gm(1), suggested the presence of a Gm(1) frequency gradient, which probably extended southwards into England. Analysis of the data also disclosed an apparently significant positive correlation between Gm(1) and blood group A frequencies (Izatt, 1971).

The study has now been extended to include the related factor, Gm(2). Figure 1 shows the locations of Scottish mainland towns and cities from which random samples of sera from blood donors were submitted to simultaneous Gm(1) and Gm(2) allotyping tests. In all, some 6000 subjects were tested. Each donor's ABO phenotype was also recorded.

Three island communities were also sampled. The investigation of the Gm allotypes in Stornoway (Fig. 1, 33) formed part of a study of the HL–A and other polymorphic systems in Lewis, an island of the Outer Hebrides (Dick, Crichton, Ferguson-Smith and Izatt, 1972). The samples from the Orkney (Fig. 1, 34) and from the Shetland Islands (Fig. 1, 35) were collected and grouped by the Glasgow Regional Transfusion Centre during a survey sponsored by the Multiple Sclerosis Society. Their ABO and Rhesus (D) blood group distributions were commented on by Brown (1965), but this is the first report concerning their Gm allotypes.

Allele frequencies for the ABO system were estimated using Bernstein's equations, as cited by Mourant (1954). In Caucasian populations the immunoglobulin IgGl type of heavy chain most

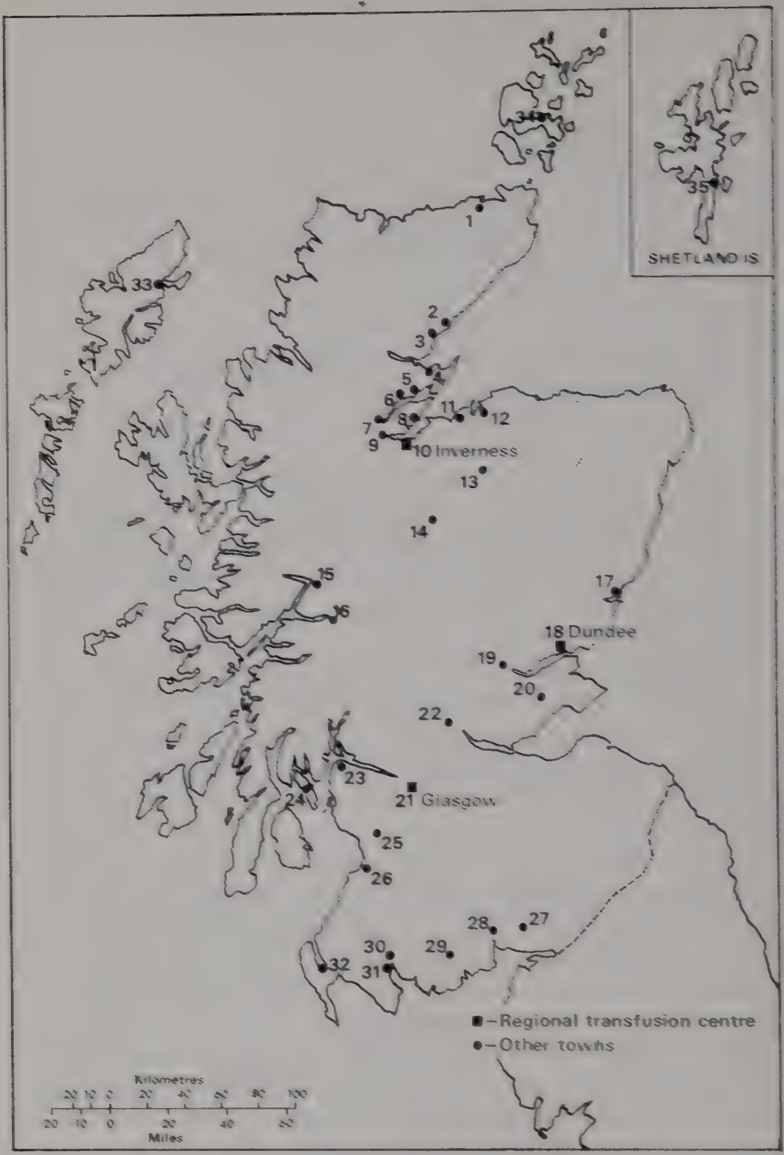

FIG. 1. Location of blood donor sessions.

commonly carries the Gm(1), or the Gm(1) and Gm(2), or the Gm(4) determinants. According to Grubb (1970), only in exceptional instances have Gm(1) and Gm(4) co-occurred on the same chain, or has Gm(2) been reported in the absence of Gm(1). For the purposes of this study the observed Gm phenotypes were therefore assumed to be under the genetic control of 3 alleles, $\underline{\mathrm{Gm}}^{1}$, $\underline{\mathrm{Gm}}^{1,\,2}$ and $\underline{\mathrm{Gm}}^{4}$. Gm allele frequencies were estimated using the following formulae:

$$\underline{\mathrm{Gm}}^{1} = p = \sqrt{\mathrm{Gm}(1, -2) + \mathrm{Gm}(-1, -2)} - \sqrt{\mathrm{Gm}(-1, -2)}$$

$$\underline{\mathrm{Gm}}^{1,\,2} = q = 1 - p - r$$

$$\underline{\mathrm{Gm}}^{4} = r = \sqrt{\mathrm{Gm}(-1, -2)}$$

Results

The ABO and IgG(Gm) allotype distribution data are set out in Table 1; the towns of Thurso (Fig. 1, 1) and Newton Stewart (Fig. 1, 30) are omitted, for their Gm(1) distributions are so different from those of their nearest neighbours that repeat sampling has been recommended (Izatt 1971).* There is a general tendency for the lower values of Gm(1, 2) to occur among the more northerly samples, and similarly for the higher frequencies of (−1, −2). In view of the pronounced differences that exist in the ABO frequencies in Scotland (Kopeć 1970) the possibility of association of Gm and ABO allele frequencies appeared worth investigation.

Gm and ABO allele frequency correlations were calculated from the data of 30 Scottish mainland towns. The Stornoway, the Orkney and the Shetland data were excluded from these calculations, for the island communities by virtue of their historical origins and geographical isolation might well not reflect a mainland trend. Of the nine possible correlations, only two were statistically significant at the 1 in 20 level of probability, and these barely so:

1. A negative correlation between $\underline{\mathrm{Gm}}^{1}$ and $\underline{\mathrm{ABO}}$ ($\underline{\mathrm{B}}$). (Correlation coefficient, $r = -0{\cdot}37$, $t = 2{\cdot}07$, 28 degrees of freedom, $0{\cdot}05 > p > 0{\cdot}025$).

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* A repeat sample of 113 specimens from Newton Stewart gives the following percentages: O 45·13, A 38·05, B 13·27, AB 3·54; Gm(1, 2) 23·89, Gm(1, −2) 31·86, Gm(−1, −2) 44·25. These results are quite consistent with those of the other Solway towns, suggesting that sampling error contributed to the apparent anomaly in the original series.

TABLE 1. IgG (Gm) and ABO blood group distributions (%)

Blood donor sessions		No.	Gm			ABO			
Ref.	Town	tested	(1, 2)	(1, −2)	(−1, −2)	O	A	B	AB
2	Brora	108	18·52	31·48	50·00	53·70	25·00	13·89	7·41
3	Golspie	100	27·00	24·00	49·00	49·00	35·00	15·00	1·00
4	Tain	230	21·74	33·91	44·35	49·13	33·48	12·61	4·78
5	Invergordon	138	29·71	25·36	44·93	52·17	28·26	13·77	5·80
6	Alness	167	20·36	32·33	47·31	54·49	32·93	9·58	2·99
7	Dingwall	185	21·08	37·30	41·62	54·59	27·57	13·51	4·32
8	Fortrose	136	18·38	36·76	44·85	50·74	35·29	12·50	1·47
9	Beauly	106	23·58	33·02	43·40	49·06	27·36	21·70	1·89
10	Inverness	633	23·06	31·28	45·66	51·34	34·28	10·90	3·48
11	Nairn	354	25·71	32·20	42·09	48·59	33·62	13·84	3·95
12	Forres	238	20·17	31·93	47·90	57·14	28·57	10·08	4·20
13	Grantown	201	19·90	37·81	42·29	48·26	40·30	9·95	1·49
14	Kingussie	142	19·01	35·92	45·07	52·11	32·39	9·15	6·34
15	Fort William	191	23·04	29·32	47·64	51·31	30·37	14·14	4·19
16	Kinlochleven	110	21·82	33·64	44·55	57·27	28·18	12·73	1·82
17	Montrose	210	24·29	30·00	45·71	53·33	34·29	10·00	2·38
18	Dundee	182	24·18	34·61	41·21	54·40	36·26	7·14	2·20
19	Perth	156	21·79	32·05	46·16	64·74	22·44	9·62	3·20

TABLE 1. (*continued*)

Blood donor sessions		No.	Gm			ABO			
Ref.	Town	tested	(1, 2)	(1, −2)	(−1, −2)	O	A	B	AB
20	Auchtermuchty	146	23·97	29·45	46·58	49·32	32·88	13·01	4·79
21	Glasgow	1000	23·00	32·30	44·70	52·40	34·60	9·90	3·10
22	Stirling	100	29·00	27·00	44·00	52·00	29·00	15·00	4·00
23	Greenock	100	24·00	33·00	43·00	54·00	33·00	10·00	3·00
24	Rothesay	100	26·00	32·00	42·00	43·00	45·00	8·00	4·00
25	Kilmarnock	100	23·00	33·00	44·00	51·00	33·00	14·00	2·00
26	Ayr	100	24·00	39·00	37·00	47·00	40·00	7·00	6·00
27	Lockerbie	100	24·00	31·00	45·00	45·00	35·00	13·00	7·00
28	Dumfries	150	22·67	32·00	45·33	46·00	41·33	11·33	1·33
29	Castle Douglas	100	27·00	33·00	40·00	55·00	34·00	8·00	3·00
31	Wigtown	145	22·76	39·31	37·93	53·79	33·79	10·35	2·07
32	Stranraer	100	22·00	36·00	42·00	52·00	30·00	11·00	7·00
	Mainland totals	5828	23·01	32·57	44·42	51·89	33·25	11·32	3·53
33	Stornoway	114	31·58	28·95	39·47	56·14	29·82	12·28	1·75
34	Orkney Isles	154	20·13	40·26	39·61	46·10	33·77	12·99	7·14
35	Shetland Isles	146	23·29	34·25	42·47	54·11	32·19	12·33	1·37

2. A negative correlation between Gm^4 and ABO (A). (Correlation coefficient, $r = -0{\cdot}39$, $t = 2{\cdot}09$, 28 degrees of freedom, $0{\cdot}05 > p > 0{\cdot}025$).

The ABO and Gm distributions in Shetland differed little from those of the Scottish mainland. Orkney was characterized by an increase in groups (B+AB) at the expense of group O: its Gm(1) frequency was raised, apparently by an increase in Gm(1, −2). Stornoway was characterized by an increase in group O at the expense of group A; its Gm(1) frequency was also raised, but apparently by an increase in Gm(1, 2) (Table 1). The significance of these observations will require to be assessed in light of the known demographic and genetic background of the island communities.

The mainland series were combined by regions, which corresponded to those served by the Scottish National Blood Transfusion Centres at Inverness, Dundee and Glasgow. The first (Inverness) was divided into two subregions since studies by Kopec (1970) indicated heterogeneity with respect to the ABO groups within it, a significantly higher incidence of groups B and AB being recorded by her in the towns Brora–Beauly (Fig. 1, 2–9) than in the towns Inverness–Kinlochleven (Fig. 1, 10–16). The third region (Glasgow) was also subdivided since Kopec noted that the City of Glasgow and part of its immediate environs (Fig. 1, 21) had higher group O and lower group A frequencies than the rest of the Glasgow region, while for the purposes of this paper a further subregion was distinguished incorporating the southern towns nearer to the Solway Firth, i.e. Lockerbie–Stranraer (Fig. 1, 27–32).

The data are set out on this regional basis in Table 2. This shows a clear tendency for Gm(1) to increase in frequency from north to

TABLE 2. Ig G(Gm) and ABO (A) group regional frequencies %

National Blood Transfusion Region	Towns Map Refs.	Number Tested	IgG Gm(1)*	ABO A
Inverness	2–9	1,170	54·70	30·85
	10–16	1,869	55·00	33·17
Dundee	17–20	694	55·19	31·84
Glasgow	21	1,000	55·30	34·60
	22–26	500	58·00	36·00
	27–32	595	57·98	35·29
Mainland total	2–32	5,828	55·58	33·25

*Gm(1) includes allotypes Gm(1, 2) and Gm(1, −2) south, and a somewhat less regular but similar trend in blood group A frequencies. Regularity of the trend is interrupted, by comparison with the rest of their region, by both the city of Glasgow (Fig. 1, 21) and the area bounding the Solway Firth (Fig. 1, 27–32) which showed reductions in Gm(1) and group A frequencies (Table 2). Glasgow City especially, but to a lesser extent the Solway area, has a pronounced Irish element in the population, and this may well account for their ABO and Gm features, for in Ireland group A frequencies are lower and group O frequencies are higher (Kopeć, 1970, Mourant 1954). Thus despite the rather arbitrary nature of the division of the country into Transfusion Service administrative regions, the negative correlation suggested between the $\underline{\text{Gm}}^{4}$ and $\underline{\text{ABO(A)}}$ alleles is discernible. However the other apparently significant correlation, that between $\underline{\text{Gm}}^{1}$ and $\underline{\text{ABO(B)}}$ allele frequencies, could not be demonstrated geographically when Scotland was divided into its Transfusion Service regions.

Before attempting any interpretation of the geographical trends and the apparent correlations between Gm and ABO frequencies, it is obviously important to obtain further data from outside Scotland, particularly from English and Welsh series. Throughout the United Kingdom the groups A and (B+AB) "varied each according to its own rule and superimposed them on group O" (Kopeć 1970). It will be of particular interest to discover whether the lowest incidence of Gm(−1) is to be found in East Anglia, which has the highest group A frequency in the United Kingdom; whether Cumberland, Westmorland, parts of Lancashire, Cheshire and East Anglia, areas all lower in group B than the rest of England, Wales and Scotland, show an increased incidence of Gm(1, −2) reflecting an increased frequency of the $\underline{\text{Gm}}^{1}$ allele; whether Welsh Gm frequencies are intermediate between those of Scotland and England. Analysis of data from these and other parts of the United Kingdom is the first step in providing an answer to these questions, and indicating whether or not the Scottish observations are fortuitous, whether they represent some functional association, or are relics of some earlier stage of genetic differentiation in the population of the country; for population migrations and invasions have undoubtedly contributed to the observed variation in present day ABO and Gm distributions throughout the world.

The biological significance of polymorphism at genetic loci is a topic of continuing interest. Many contemporary studies are being directed towards the effects on its maintenance of either natural selection or of neutral mutation followed by random drift. Earlier studies tended to concentrate on one genetic system at a time. But systems should not be studied only in isolation. Interactions must also be investigated, for selection acts on the whole phenotype and not merely on part (Harris 1971, Sing, Shreffler, Neel and Napier 1971). It may well be therefore that the gradient and correlations found here are selective in origin. With respect to the ABO polymorphism, the part played by selection through susceptibility to infectious disease is not yet clear (Otten 1967). In antibody production Grubb (1970) believes that at times the immunoglobulin locus choice may be antigen-dependent, but that antigen binding is not the only evolutionary selective force to shape Ig molecular structure. He predicted that correlations will be detected between immunoglobulin functional capacity and the Ig genetic markers, such as Gm. This paper suggests that their joint consideration may prove rewarding.

Acknowledgements

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ISOENZYME VARIATION IN NORTHUMBERLAND

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Extensive studies (Roberts 1953, Kopeć 1970) of the distribution of red cell ABO antigens have provided much information about present day genetic variation in England. Fraser Roberts, with a considerable sample size from the northern counties of England, showed a clear distinction in ABO blood group frequencies along a line cutting across south Northumberland, the north part of County Durham and through Cumberland. The studies of Kopeć showed very close correspondence with the findings of Roberts in the location of the line in south Northumberland and also elucidated other regional differences in the northern counties. The ABO gene frequency distribution showed a highly significant difference between the south east of Northumberland and the remainder of the county. Independent evidence comes from the study of Sunderland (1966) who observed variation in the gene frequencies of the PTC tasting polymorphism between these two zones of Northumberland. For the interpretation of present day genetic variation, historical population movements were studied by Dobson and Roberts (1971) who showed relatively little gene flow in Northumberland in the eighteenth century, which may have been sufficiently slight to allow the maintenance of any differences that existed in gene frequencies between the two zones. Today with the great development of laboratory techniques that has occurred, it is possible to detect many more genetically controlled characters showing frequency differences among populations. The present study was initiated for two purposes, to enquire whether other genetic characters demonstrate the same frequency differences among localities of Northumberland as is shown by the ABO groups and secondly to establish normal gene frequencies in the region against which the frequencies in various disease groups could be compared. Seven genetically determined red cell isoenzyme systems, controlled by eight independent loci, were studied.

Material and Methods

Blood Specimens

Blood specimens were obtained both from normal individuals who had consented to act as controls in one or other of the surveys of gene frequencies in particular diseases, currently in progress in this Laboratory, and from blood donors, the specimens being made available for the same purpose by Dr. Murray from the Regional Blood Transfusion Centre, Newcastle. The subjects were all born in Northumberland and the sampling graticule was designed to cover 109 birth localities from all over the county. Unfortunately the sample numbers from each locality could not be exactly regulated, but all localities originally intended for inclusion were in fact represented. Adjacent localities were pooled to coincide with the unit areas located in Kopec's study. These were subsequently divided into six zones, two each from north Northumberland, southeast Northumberland and southwest Northumberland (Fig. 1), the dividing line between southeast Northumberland and the remainder of the county coinciding with Kopec's line of ABO frequency distinction.

In all, 550 blood specimens were available for examination. After the initial blood grouping, sera were removed and stored for later analysis and the red cell lysates were prepared by washing twice with normal saline and once with 1·2 per cent saline. The lysates were stored at −30°C until analysis of all enzyme systems was complete.

Laboratory Techniques

Horizontal starch gel electrophoresis was performed for identification of the various isoenzymes, using gels of 9 per cent BDH hydrolyzed starch (Smithies). All electrophoretic procedures were carried out in the cold room at 4°C–5°C. The fresh lysates were immediately tested for adenosine deaminase by the method of Spencer *et al.* (1968). By changing the enzyme substrate, glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase were typed on the same gel, as described by Bowman and Ronaghy

(1967). For the separation of these enzyme systems, a phosphate buffer pH7 was employed, according to Fildes and Parr (1963). One portion of this gel was stained for lactic dehydrogenase. Adenylate kinase was examined by the method of Fildes and Harris (1966) and acid phosphatase was tested by the discontinuous buffer system as given by Hopkinson *et al.* (1964). Phosphoglucomutase was typed using double the molar concentration of all ingredients of the buffer given by Spencer *et al.* (1964) at pH7·4.

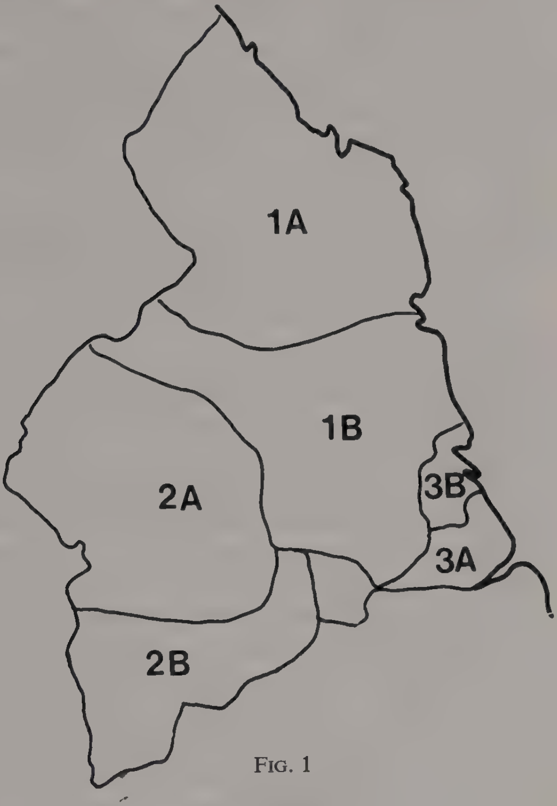

FIG. 1

Results

Adenosine Deaminase (ADA)

The polymorphic existence of this aminohydrolysate enzyme (E.C. No. 3.5.4.4) in man was established by Spencer *et al.* (1968). Three commonly occurring phenotypes were identified, two homozygous (ADA1.1 and ADA2.2) and a heterozygous (ADA2.1). The

TABLE 1. Adenosine deaminase in Northumberland

Locality	No.	Phenotype Numbers						Gene frequency	
		1.1		2.1		2.2		ADA^1	ADA^2
		Observed	Expected	Observed	Expected	Observed	Expected		
North Northumberland A	92	78	78·5	14	12·9	0	0·5	0·924	0·076
B	94	86	86·2	8	7·7	0	0·2	0·957	0·043
West Northumberland A	53	47	47·2	6	5·7	0	0·2	0·943	0·057
B	25	20	20·2	5	4·5	0	0·3	0·900	0·100
Southeast Northumberland A	108	92	91·7	15	15·7	1	0·7	0·921	0·079
B	97	84	84·4	13	12·1	0	0·4	0·933	0·067
Total	469	407	408·1	61	58·8	1	2·1	0·933	0·067

previous study in the English population and the present study suggest a very low frequency of phenotype ADA2.2, occurring in approximately 1 in 450 of English subjects. Further studies added two new phenotypes to the literature, 3.1 by Hopkinson *et al.* (1969) and 4.1 by Ritter *et al.* (1971). There is however a discrepancy in the photographic depiction of the 3.1 phenotype in these studies. In the Northumberland study only the three common phenotypes are encountered (Table 1). Out of 469 samples tested, the ADA2 gene frequency is approximately 7 per cent in Northumberland. This is higher than the value of 5 per cent given by Hopkinson *et al.* (1969) for their English sample, significantly so (χ^2 4·64 with 1 degree of freedom). The variation can perhaps be accounted for by region of origin of samples, with Hopkinson's material deriving predominantly from the south.

The apparent range of ADA2 gene frequency in the six sub-regions of Northumberland, from 4–10 per cent, is not significant, but suggests that further enquiry may be profitable.

6-Phosphogluconate Dehydrogenase (6PGD)

Polymorphism of 6PGD (E.C. no. 1.1.1.4.1) was initially studied by Parr (1966). Eight phenotypes were characterized by the isozyme pattern and their enzymatic activity for 6PGD and, of these, five were observed in Parr's English sample of 4558 subjects, AA, CA, CC, RA and HA distinguished by the isozyme pattern. The incidence of the normal pattern (the homozygous phenotype AA) was 95 per cent in his sample. Next highest in frequency is the common variant, sometimes known as the Canning heterovariant, phenotype CA, and for this the frequency was approximately 4 per cent.

The present survey showed that 96 per cent of individuals were of the normal pattern, and the only variant form was phenotype CA. (Table 2). The PGD^C gene frequency is approximately 2 per cent. This is slightly lower than the frequency observed in Parr's series, but not significantly so. The gene frequency in the six sub-regions ranges from less than 1 per cent to 5 per cent, but again this heterogeneity is not significant.

Adenylate Kinase (AK)

Variation in the enzyme adenylate kinase (ATP-AMP phosphotransferase; E.C. No. 2.7.4.3) was studied in an English sample by Rapley *et al.* (1967), after earlier studies by Fildes and Harris

TABLE 2. 6-Phosphogluconate dehydrogenase in Northumberland

Locality	No.	Phenotype numbers						PGD^A	PGD^C
		A		CA		CC			
		Observed	Expected	Observed	Expected	Observed	Expected		
North Northumberland A	134	132	132·0	2	2·0	0	0·0	0·993	0·007
B	98	94	94·0	4	3·9	0	0·0	0·980	0·020
West Northumberland A	61	60	60·0	1	1·0	0	0·0	0·992	0·008
B	28	25	25·1	3	2·8	0	0·1	0·946	0·054
Southeast Northumberland A	109	105	105·1	4	3·9	0	0·0	0·982	0·018
B	119	110	110·2	9	8·7	0	0·2	0·962	0·038
Total	549	526	526·3	23	22·5	0	0·2	0·979	0·021

TABLE 3. Adenylate kinase in Northumberland

Locality	No.	Phenotype numbers						Gene frequency	
		1.1		2.1		2.2		AK^1	AK^2
		Observed	Expected	Observed	Expected	Observed	Expected		
North									
Northumberland A	134	128	128·1	6	5·9	0	0·1	0·978	0·022
B	98	90	90·2	8	7·7	0	0·2	0·959	0·041
West									
Northumberland A	61	58	58·0	3	2·9	0	0·0	0·975	0·025
B	28	27	27·0	1	1·0	0	0·0	0·982	0·018
Southeast									
Northumberland A	109	105	105·0	4	3·9	0	0·0	0·982	0·018
B	119	116	116·0	3	3·0	0	0·0	0·987	0·013
Total	549	524	524·3	25	24·4	0	0·3	0·977	0·023

TABLE 4. Acid phosphatase in Northumberland

		Phenotype numbers											Gene frequencies			
Locality	No.	A		B		BA		CB		CA		C	P_a	P_b	P_c	χ^2
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Exp.				
North Northumberland A	134	12	12·9	52	54·6	56	53·0	11	8·9	3	4·3	0·4	0·310	0·638	0·052	0·37
B	98	13	12·9	31	31·4	40	40·2	9	7·9	5	5·1	0·5	0·362	0·566	0·071	0·22
West Northumberland A	62	4	5·2	25	25·8	25	23·2	5	5·2	3	2·3	0·3	0·290	0·645	0·065	0·45
B	29	2	1·9	12	13·1	11	10·1	4	2·7	0	1·0	0·1	0·259	0·672	0·069	0·19
Southeast Northumberland A	109	14	13·2	43	42·4	46	47·4	4	3·7	2	2·1	0·1	0·349	0·624	0·027	0·10
B	117	19	15·1	45	41·9	43	50·3	7	6·0	3	3·6	0·2	0·359	0·598	0·043	2·3
Total ..	549	64	60·7	208	208·7	221	225·0	40	34·5	16	18·6	1·4	0·332	0·617	0·051	2·89

(1966) had shown three common phenotypes (AK1, AK2.1 and AK2) of this enzyme in a population, under the control of two genes (AK1 and AK2). Rare phenotypes 3.1 and 4.1 were described by Bowman *et al.* (1967), for which the genes AK3 and AK4 are very rare. In the study of Rapley *et al.* the frequency of the AK2 gene was about 4½ per cent in the British population. This estimate was based on a sample size of 1887 individuals, including the 960 specimens of Fildes and Harris (1966). The present survey clearly shows a lower frequency of the AK2 gene (approximately 2 per cent) in Northumberland, (Table 3) significantly lower than in the sample of Rapley *et al.* (χ^2 10·2 with 1 degree of freedom). Again the difference may well be due to the different regions of origin of the samples. The range of frequencies of the AK2 gene in the six sub-regions of Northumberland is quite narrow (approximately 1–4 per cent) and this variation is not significant.

Acid Phosphatase (AP)

Human red cell acid phosphatase (E.C. No. 3.1.2.3) polymorphism was described by Hopkinson *et al.* (1963). Three allelic autosomal genes P^a, P^b and P^c are responsible for six phenotypes in European populations A, BA, B, CA, CB and C. Phenotype C is very rare in the British population (approximately 1 in 600), and almost all the P^c genes manifest in the heterozygotes CA and CB. On a sample of 367 British specimens Hopkinson *et al.* (1964) obtained a P^c gene frequency of 4 per cent derived from 28 heterozygotes. In the present study (Table 4) the P^c gene frequency is very similar, approximately 5 per cent. There is no significant difference between the frequencies of acid phosphatase types in the two studies (χ^2 5·61 with 3 degrees of freedom). The P^c gene frequency ranges from 2·7 to 7·2 per cent in the six Northumberland sub-samples, and the P^a gene frequency 26 per cent to 36 per cent, but the six sub-regions are not significantly heterogeneous (χ^2 6·65 with 6 degrees of freedom).

Phosphoglucomutase (PGM)

Phosphoglucomutase (α-D glucose 1 : 6 diphosphate, α-D glucose 1 phosphate transferase: E.C. No. 2.7.5.1) is an enzyme which presents a highly polymorphic appearance in human red cells. It is distinguished by its multiple components on starch gel separations. Three independent loci have been established as governing this

TABLE 5. Phosphoglucomutase (locus I) in Northumberland

Locality	No.	Phenotype numbers						Gene frequency		χ^2
		1.1		2.1.		2.2		PGM¹	PGM²	
		Observed	Expected	Observed	Observed	Observed	Expected			
North Northumberland A	134	85	83·8	42	44·3	7	5·9	0·791	0·209	0·34
B	98	65	61·3	25	32·4	8	4·3	0·791	0·209	0·6
West Northumberland A	61	35	33·9	21	23·1	5	3·9	0·746	0·254	0·07
B	29	10	10·6	15	13·9	4	4·6	0·603	0·397	0·05
Southeast Northumberland A	109	65	63·2	36	39·6	8	6·2	0·761	0·239	0·90
B	118	67	69·4	47	42·2	4	6·4	0·767	0·233	1·5
Total	549	327	321·3	186	197·4	36	30·3	0·765	0·235	1·83

polymorphism. As many as twelve phenotypes have been characterized for PGM locus 1 (Hopkinson and Harris 1966) but three phenotypes (PGM1, 2–1, and 2) occur in any population. These phenotype differences are controlled by a pair of autosomal alleles, PGM^1 and PGM^2. Specimens from 2115 subjects were typed for PGM locus 1 variants (Hopkinson and Harris 1966) and six rare phenotypes were found, heterozygous combinations of rare alleles with one or other of the common PGM1 and PGM2 alleles. The present survey on 549 persons typed for PGM locus 1 variants (Table 5) showed a value of 23 per cent for the PGM^2 gene frequency in Northumberland. This is the same value as in the sample of Hopkinson and Harris (1966), ($\chi^2 = 1 \cdot 19$ with 2 degrees of freedom). There may well be variation of gene frequency in the Northumberland sub-regions, for the elevated frequency of the PGM^2 gene appearing in southwest Northumberland approaches significance.

Phosphoglucomutase Locus II, Lactic Dehydrogenase (LDH) and Glucose-6-Phosphate Dehydrogenase (G6PD)

In the present survey no enzyme variants controlled by the PGM locus II alleles appeared (Table 6), a result similar to the findings of Hopkinson and Harris (1966) which did not show any variants. It appears that the ${PGM_2}^1$ gene is fixed at a unit frequency in the British population. Davidson *et al.* (1965) tested 1015 random specimens from English subjects for LDH, and gave an incidence of 0·002 LDH variants in the English population. In the present study no LDH variants were observed in Northumberland. It seems that

TABLE 6. Numbers tested for phosphoglucomutase locus II(PGMII), glucose 6 phosphate dehydrogenase (G6PD), and lactic dehydrogenase (LDH). All PGMII results 1–1, all isozyme patterns for LDH normal and G6PD normal B phenotype

Locality		Number tested for		
		PGM (Locus II)	G6PD	LDH
North Northumberland	A	134	134	134
	B	98	98	98
West Northumberland	A	61	61	61
	B	29	28	28
Southeast Northumberland	A	109	109	109
	B	119	119	119

the variant forms found by Davidson *et al.* (1965) are restricted to certain English families. The study of G6PD by Beutler *et al.* (1968) and the present study of Northumberland showed similar results in that no variant types were detected, all subjects having the electrophoretic mobility of G6PD type B.

Discussion

Work so far is to be regarded essentially as a pilot study, to see whether more intensive investigation is likely to be rewarding. To expect to demonstrate conclusive heterogeneity among subsamples of the present size would be optimistic indeed. It is not the lack of significant heterogeneity among the subsamples that should be emphasized therefore, but the quite appreciable range of gene frequency that they suggest, in 6PGD and phosphoglucomutase particularly. Similarly discussion of the lack of significance of the difference in isoenzyme gene frequencies on either side of the line dividing southeast Northumberland from the remainder of the county by ABO blood groups needs to recognize that the samples consist respectively of some 220 and 330 subjects. These numbers are to be compared with the 25,000 on which Dr. Kopec's highly significant distinction of southeast Northumberland from the remainder of the county and from north Durham was based, and the still greater numbers in Fraser Roberts' study.

On the positive side, however, taking the sample from Northumberland as a whole, there appear clear differences in at least two systems from the frequencies reported elsewhere in the country, significant in adenosine deaminase and highly so in adenylate kinase. Once again Northumbrian folk are shown to be different, just as in their ABO frequencies. The reason for this difference is not at all clear. Difference in selection pressures, random changes in gene frequency at a time when the population size was much less than it is today, these are possible. It remains a possibility also however that the differences are relics of the historical settlement of the country, and comparison with other northwest European peoples would be of interest. For example when the ADA frequencies of the Northumberland sample are compared with the other English sample of Hopkinson the difference is significant, but when the Northumbrian series is compared with a Danish sample of Dissing and Knudsen (1970) there is no significant difference. For adenylate kinase the London sample of Rapley *et al.* (1967) is practically identical in frequency to the Norwegian sample of Berg (1969), but Swedish (Skude and Jakobsson 1970) and Danish (Lamm 1971) samples give slightly higher frequencies of phenotype 1–1, and the Northumbrian series gives the highest frequency of this phenotype in northwest Europe. It is possible therefore that the Northumbrian frequencies owe something to the settlers from across the North Sea of over a thousand years ago. Certainly no affinity with the Irish, (Palsson *et al.* 1970) as representatives of the earlier settlers in Britain, appears. Though there is some similarity in ADA1–1 between the Irish and Northumberland series, the distribution of phenotypes for acid phosphatase is quite different, and those for phosphoglucomutase and adenylate kinase show the Irish to be at the opposite end of the northwest European spectrum from the Northumberland results. This type of exercise is interesting, but definitive results must await more comprehensive comparison with other samples from northwest Europe, and as yet there are relatively few of these available.

Acknowledgements

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Summary

Study of red cell isoenzymes in some 550 subjects born in Northumberland suggest differences in gene frequency from the south of England. When the sample is further analysed by locality no significant differences within Northumberland appear, but the subsamples are small and examination of a larger series seems warranted.

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A LOCAL ORKNEY POLYMORPHISM– ERYTHROCYTE INDOPHENOL OXIDASE FREQUENCIES

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Introduction

In the past few years many human erythrocyte enzymes have been detected after starch gel electrophoresis by the use of specific histochemical stains (Giblett, 1969: Shaw and Prasad, 1970). Many of these enzymes have been shown to exhibit genetic variation (Giblett 1969: Harris 1969a, b). Where the enzyme being studied is a dehydrogenase, or its reaction can be linked via a dehydrogenase, many of the stains used for its detection after electrophoresis contain the electron carrier phenazine methosulphate (PMS) and a tetrazolium salt (MTT), the latter being reduced at the site of enzyme activity to a blue insoluble formazan deposit. It has often been observed that when starch gels are stained with a mixture containing both PMS and MTT, in addition to the blue bands of formazan deposited at the site of the enzyme under investigation, light or achromatic hands are produced by many tissue extracts including erythrocytes. The protein responsible for these achromatic bands has the property to oxidize, or at least maintain in an oxidized form, tetrazolium salts in the presence of phenazine methosulphate and light. The nature of this enzyme has not been precisely identified, but since it has been found to be capable of oxidizing 2,6-dichlorophenolindophenol, it was provisionally called indophenol oxidase (Brewer, 1967). More recently it has been referred to as tetrazolium oxidase (Baur and Schoor, 1969).

Surveying many thousands of human haemolysates, Brewer (1967) found only one specimen with an altered electrophoretic pattern.

The haemolysate from the propositus showed, instead of the one major electrophoretic component, three major bands of indophenol oxidase activity. Further examples of the variant phenotype were found amongst the relatives of the propositus. It was suggested that these individuals were heterozygous for an extremely rare allele at an autosomal gene locus. Whereas the human indophenol oxidase presents a common electrophoretic pattern throughout the human species except for rare genetic variants, this is not the case in dogs, for a genetic polymorphism of indophenol oxidase in canine erythrocytes has been demonstrated by Baur and Schoor (1969). More recently a number of isolated reports of rare genetic variants of the human erythrocyte enzyme have appeared in the literature (Baur, 1969: Shinoda, 1970: Hopkinson and Harris, 1971). In all these cases the incidence of the variant genotype (heterozygote) has been less than 1 in 1000.

It is well known that small isolated populations may show unusual gene frequencies. It appeared worthwhile therefore to enquire whether the variants of this enzyme showed an aberrant frequency in the remote Orkney islanders. This paper presents the results for the population of Westray and North Ronaldsay islands of the Orkneys,

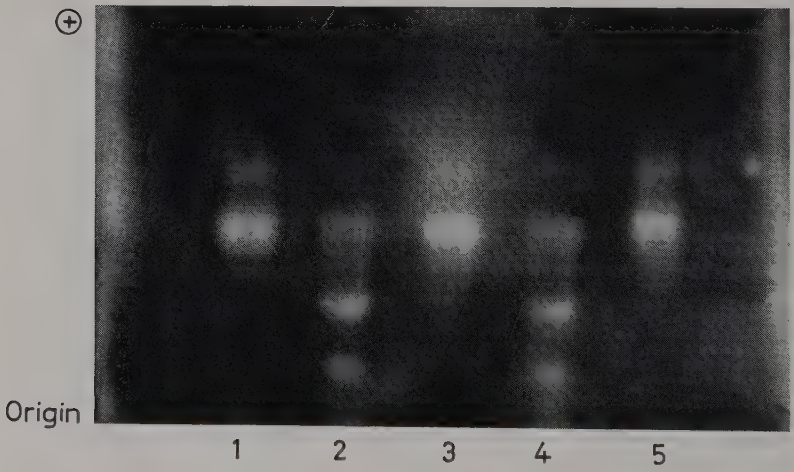

FIG. 1. Photograph of starch gel showing the Westray variant of red cell indophenol oxidase. Sample 1, 3, 5: Usual type. Sample, 2, 4: Westray variant

and compares them with frequencies in other samples from Britain (London and southern Ireland) and elsewhere.

Materials and Methods

Haemolysates for starch gel electrophoresis were prepared by lysing 0·1 ml of saline-washed red cells in 0·2 ml of distilled water. The haemolysates were centrifuged at 2000 × g for 10 minutes. Horizontal starch gel electrophoresis was carried out at pH 6·8 in 0·01 *M* sodium phosphate buffer, with 0·2 *M* sodium phosphate in the bridge compartments. The samples were inserted into the gels using inserts of Whatman No. 17 filter paper. The electrophoresis was carried out at 24 volts per cm for 3 hours. A constant temperature was maintained by the use of aluminium cooling plates through which water at 8°C was circulated.

The gels were sliced and stained for indophenol oxidase with a solution containing 10 ml 0·3 *M* Tris-HCl pH 8·0, 2·0 mg PMS and 2·0 mg MTT. The gels were incubated at room temperature whilst being exposed to the light. After about 30 minutes most of the surface of the gel had turned blue (due to the photooxidation of MTT) except for the achromatic areas of indophenol oxidase activity.

Results

Blood specimens were obtained from 406 residents on the island of Westray and 56 on North Ronaldsay (Orkneys), as part of a survey of the inhabitants of a number of the islands of the Orkney group. Blood was not taken from any individual where both parents had already been sampled. Two samples from elsewhere in Britain were examined for comparison. One from southern Ireland consisted of 260 individuals, part of the Irish sample of which a report is given on pp. 141–159 of this volume. The second, a large mixed sample of 2500 subjects, was drawn from the many inpatients and outpatients attending the London Hospital, all London residents, the majority of whom are of English origin.

Of the 406 samples from Westray, 394 showed a single anodically migrating band of indophenol oxidase. The remaining 12 exhibited the variant electrophoretic pattern shown in Figure 1. Family studies confirmed that the variant pattern was genetically determined and, for the Westray population, the results are in close agreement with those predicted on the Hardy-Weinberg hypothesis (Table 1). So far a direct physicochemical comparison has not been made between the Westray variant and any of the other rare phenotypes described in the literature. The variant has not yet appeared in the small sample from North Ronaldsay. It is absent from the Irish and London samples, suggesting that the Westray folk may be genetically different from populations elsewhere in Britain. In addition to these samples, others from non-European populations were examined; 160 specimens from Ethiopia and some 300 from Papua. The results of this work, as well as other published results, are summarized in Table 2.

TABLE 1. The distribution of red cell indophenol oxidase phenotypes in the population of Westray

	Number observed	Number expected
Usual type	394	393·5
Westray heterozygote	12	12·2
Westray homozygote	0	0·2

TABLE. 2 The incidence of indophenol oxidase variants in a number of human populations

Population	Number examined	Number of electrophoretic variants	Frequency of the most common allele
Westray (Orkney)	406	12	0·985
North Ronaldsay (Orkney)	56	0	1·000
Southern Ireland	260	0	1·000
London-mixed	2500	0	1·000
Papua	301	0	1·000
Ethiopia	160	0	1·000
Japan (Shinoda, 1970)	5000	1	0·9999
United States (Brewer, 1967)	many thousand	1	0·9999
Europeans (Hopkinson and Harris, 1971)	6500	5	0·9996

Discussion

The small amount of data at present available on the incidence of indophenol oxidase variation suggests that in most populations mutant alleles are either extremely rare or absent. The discovery of the Westray variant allele at a frequency sightly in excess of 1 per cent is therefore the exception rather than the rule. Whilst being present at a polymorphic frequency in Westray island, it was not detected in the nearby island of North Ronaldsay and this suggests that the polymorphism may be of curiously local occurrence. In a small island community such as Westray (population about 800), some degree of common ancestry and inbreeding is to be expected, and it may well be that a number of the individuals with the variant phenotype may be not too distantly related.

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OBSERVATIONS ON ABH SECRETION AND LEWIS TYPES

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Introduction

The antigens A, B and H of the ABO blood group system are not confined to the red cells but are found in a soluble form in the body fluids. Not all individuals, however, secrete their corresponding ABH substances; a proportion are non-secretors—that is, their fluids are free from or contain only trace amounts of these substances. It is considered that the secretion of the ABH group-specific substances is controlled by a pair of allelomorphic genes, Se and se. Three types of individual are therefore possible—SeSe, Sese and sese. The first two are secretor and the third is a non-secretor.

There is an association between the secretion of ABH blood group substances and the Lewis blood group system in that, excluding rarities, individuals whose red cells type as Le (a + b −) fall into the non-secretor category, while those whose red cells are Le (a − b +) are secretors. There are therefore available two independent tests for secretor status: (a) a test on a body fluid, usually saliva, and (b) a test for the Lewis type of the red cells. A small proportion of the population have red cells which type as Le (a − b −) and these can be either secretors or non-secretors. Their secretor status has to be determined on their body fluids.

Although the figures most quoted for secretor/non-secretor frequencies in the British Isles are those of McConnell (Race and Sanger 1968), which show a non-secretor frequency of 22·7 per cent, other figures quoted by Mourant (1954) from some otherwise unpublished observations of Ikin *et al.* (1952) strongly suggested that this general figure of 22·7 per cent might not hold for the Irish and

Scottish. The fact that these ethnic groups probably have higher non-secretor frequencies can be derived from the frequencies Ikin *et al.* found for Le (a + b −) since among 527 Scottish individuals and 106 Irish, 28·46 per cent and 31·13 per cent respectively were of this type. The corresponding saliva specimens were apparently not tested but it may be assumed that all the Le (a + b −) individuals were non-secretors, and in addition, a small number of non-secretors would be expected in the Le (a − b −) phenotype. A series of 531 salivas from schoolchildren in Belfast showed a non-secretor frequency of 26·55 per cent (Dodge 1967). These various results suggested that a survey of the ABO groups and secretor status of individuals from various parts of the British Isles might show more variation than had been generally accepted.

A search of the literature reveals but few secretor/non-secretor samples showing such a high percentage of non-secretors as those of Ikin for the Irish and Scottish based on Lewis types. Van Arsdel (1958) in testing a series of 3144 students from the University of Washington, found the proportion of non-secretors to be 24·11 per cent. Nerell (1964) collected together the figures of 12 investigated populations of provenance as diverse as Egypt and Canada with frequencies of non-secretors ranging from 11·1 per cent to 25·4 per cent. Several series from India show higher non-secretor frequencies than have been found generally in Europe. Pradhan *et al.* (1970) found 28·17 per cent non-secretors among medical students at Kanpur.

Donors and Methods

Our series comprises 284 individuals from the staff of the North and South London Regional Transfusion Centres and the London Hospital, 550 blood donors from Aberdeen, 644 from Belfast, 597 from Dublin and 352 individuals from the Island of Westray in the Orkneys. The blood donors from the Aberdeen, Belfast and Dublin Transfusion Centres were collected from surrounding towns as well as from the named centres. The ABO groups of the London and the Westray donors were randomly selected but the selection from the Blood Transfusion Centres was made according to the requirements of the blood banks.

It was not possible to obtain both red cells and saliva samples from every individual included in the series. Not all the Irish and

Scottish blood donors contributed samples of saliva; from Aberdeen, Belfast and Dublin there were respectively 44, 100 and 162 fewer saliva than blood samples obtained. No saliva samples were collected from the Westray donors. The London series included saliva samples from 71 individuals whose ABO groups were known but whose red cells were not tested with anti-Le^a and anti-Le^b sera. One of us (P.J.L.) carried out the Lewis typing of the red cells at the Aberdeen, Belfast and Dublin Centres, but saliva samples from these centres were frozen within a few hours of collection and tested in our own laboratory. The blood samples from the Westray donors were flown to London and reached our laboratory 48–72 hours after collection.

ABO typing was carried out by a standard tube technique examining cells and serum independently. The Lewis types were determined by a similar tube technique but the tests were incubated in a water bath at 15°C for 2 hours. The anti-Le^a and anti-Le^b sera were well established reagents kindly supplied by the South London Regional Blood Transfusion Centre. Saliva samples diluted 1 in 2 in saline were boiled in a water bath for 15 minutes followed by centrifugation before being examined for the presence of A, B and H substances. A screening inhibition technique was devised and each sample was tested against suitably diluted anti-A, anti-B and ant-H reagents. The anti-A and anti-B were of human origin while the anti-H was the plant lectin Ulex europaeus.

Results and Discussion

A comparison of the frequencies of secretors and non-secretors for each centre and for the individual collection areas is shown in Table 1.

The secretor/non-secretor frequencies obtained for the London series are not significantly different from those of McConnell (Race and Sanger 1968) for Liverpool, which are usually taken as standard for England. His values for these gene frequencies are 0·4767 for se and 0·5233 for Se.

However, the Scottish and Irish values are strikingly different and are among the highest frequencies of non-secretors on record. The total observed numbers of secretors and non-secretors at the Dublin and Belfast Centres were amalgamated to give a figure for the Irish. Our London series was added to the large English series reported

TABLE 1. Frequencies of secretors and non secretors

Centre	Collection area	Total tested	Secretors		Non secretors		Gene frequencies	
							se	Se = (1–se)
Aberdeen	Keith	148	102	(68·92%)	46	(31·08%)	0·5575	0·4425
	Turriff	193	138	(71·51%)	55	(28·49%)	0·5337	0·4663
	Banchory	103	72	(69·91%)	31	(30·09%)	0·5486	0·4514
	B.T.C.	66	46	(69·70%)	20	(30·30%)	0·5505	0·4495
	Total	510	358	(70·20%)	152	(29·80%)	0·5459	0·4541
Belfast	*Gallahers	48	35	(72·92%)	13	(27·08%)	0·5204	0·4796
	**Howard St.	123	88	(71·55%)	35	(28·45%)	0·5334	0·4666
	B.T.C. staff	36	26	(72·23%)	10	(27·77%)	0·5270	0·4730
	*AEI	108	82	(75·93%)	26	(24·07%)	0·4907	0·5093
	*Andrewes	31	22	(70·97%)	9	(29·03%)	0·5388	0·4612
	*Dundonald House	66	48	(72·73%)	18	(27·27%)	0·5223	0·4777
	Ballymoney	120	71	(59·17%)	49	(40·83%)	0·6390	0·3610
	Total	532	372	(69·92%)	160	(30·08%)	0·5484	0·4516
Dublin	Kildare	160	114	(71·25%)	46	(28·75%)	0·5362	0·4638
	*CIE	162	110	(67·91%)	52	(32·09%)	0·5665	0·4335
	B.T.C.	113	71	(62·84%)	42	(37·16%)	0·6096	0·3904
	Total	435	295	(67·82%)	140	(32·18%)	0·5673	0·4327
London	London	284	215	(75·70%)	69	(24·30%)	0·4929	0·5071

B.T.C.—Blood Transfusion Centre.

* Place of employment.

** Blood Transfusion collection centre in Belfast.

TABLE 2. Lewis types of red cells

Centre	Collection area	Total tested	Le (a+b−)	Le (a−b+)	Le (a−b−)
Aberdeen	Keith	161	41 (25·46%)	109 (67·70%)	11 (6·83%)
	Turriff	210	62 (29·52%)	138 (65·71%)	10 (4·76%)
	Banchory	107	31 (28·97%)	72 (67·28%)	4 (3·73%)
	B.T.C.	76	23 (30·26%)	48 (63·15%)	5 (6·57%)
	Total	554	157 (28·33%)	367 (66·24%)	30 (5·41%)
Belfast	*Gallahers	57	14 (24·56%)	40 (70·17%)	3 (5·26%)
	**Howard St.	132	35 (26·51%)	81 (61·36%)	16 (12·12%)
	B.T.C. staff	36	10 (27·77%)	26 (72·22%)	0
	*AEI	138	32 (23·18%)	99 (71·73%)	7 (5·07%)
	*Andrewes	35	11 (31·42%)	24 (68·57%)	0
	*Dundonald House	120	27 (22·50%)	83 (69·16%)	10 (8·33%)
	Ballymoney	114	44 (38·59%)	58 (50·87%)	12 (10·52%)
	Total	632	173 (27·37%)	411 (65·03%)	48 (7·59%)
Dublin	Kildare	248	59 (23·79%)	175 (70·56%)	14 (5·64%)
	*CIE	186	53 (28·49%)	121 (65·05%)	12 (6·45%)
	B.T.C.	163	53 (32·51%)	89 (54·60%)	21 (12·88%)
	Total	597	165 (27·63%)	385 (64·48%)	47 (7·87%)
London	London	213	49 (23·00%)	134 (62·91%)	30 (14·08%)
Westray	Westray	352	111 (31·53%)	171 (48·58%)	70 (19·89%)

B.T.C.—Blood Transfusion Centre.
* Place of employment.
** Blood Transfusion collection centre in Belfast.

by Horwich *et al.* (1966), in which 2435 people were tested of whom 590 (24·23 per cent) were non-secretors. The English and Irish figures were then compared by means of 2×2 tables. A χ^2 value of 20 was obtained; $p < 0 \cdot 001$ for 1 degree of freedom. Comparing the Aberdeen figures with the English figures in the same way gives a chi-squared of 8·3 ($0 \cdot 001 < p < 0 \cdot 01$ for 1 degree of freedom). Recently, frequencies similar to the Irish and Scottish have been shown to obtain in Iceland (Thordarson, Bjarnason, Lincoln and Dodd 1972).

The breakdown of the centres into the various collection areas is also shown in Table 1. In general there is a high degree of homogeneity but the few exceptions are noteworthy. For instance at the Belfast Centre, the individuals collected from the engineering firm of AEI show a frequency of 24·07 per cent of non-secretors which is very similar to the London figure. This is probably due to the high proportion of English individuals employed by this firm. In contrast, a strikingly high frequency (40·83 per cent) of non-secretors was found in testing 120 individuals from the market town of Ballymoney.

Table 2 shows the results of the Lewis typing of the red cells of all individuals from whom red cell samples were obtained irrespective of whether or not there was a corresponding saliva sample. There is a close correlation between the frequency of the Le $(a+b-)$ type and the frequency of non-secretors shown in Table 1. Also, these results are very similar to the findings of Ikin (Mourant 1954). Among the Westray samples, the frequency of the Le $(a+b-)$ type (31·53 per cent) is the highest frequency of all the Centres.

The Le $(a-b-)$ type was sometimes difficult to distinguish. Some examples of group A_1 secretors possessing Le^b may have been scored as Le $(a-b-)$ because of the well-known inability of some anti-Le^b sera to disclose the presence of Le^b when accompanied by A_1. However, the anti-Le^b we used gave at least weak reactions with the red cells of most group A_1 secretors.

The distribution of the Lewis types among the ABO groups for each centre is shown in Table 3. As expected, at all the Centres the frequency of the Le $(a-b-)$ type tends to be highest in the A and AB groups. If the Le, le and Se, se genes segregate independently the secretor/non-secretor ratio in the Le $(a-b-)$ phenotype should reflect that of the rest of the population. Taking the London, Aberdeen, Belfast and Dublin centres together (there were no saliva

TABLE 3. Distribution of Lewis type among the ABO groups

Centre	ABO group	Total tested	Le (a+b−)		Le (a−b+)		Le (a−b−)	
London	O	102	27	(26·47%)	67	(65·68%)	8	(7·84%)
	A	84	18	(21·42%)	48	(57·14%)	18	(21·42%)
	B	23	3	(13·04%)	17	(73·91%)	3	(13·04%)
	AB	4	1	(25·00%)	2	(50·00%)	1	(25·00%)
Aberdeen	O	271	82	(30·25%)	178	(65·68%)	11	(4·05%)
	A	211	58	(27·48%)	136	(64·45%)	17	(8·05%)
	B	49	8	(16·32%)	38	(77·55%)	3	(6·12%)
	AB	19	6	(31·57%)	9	(47·36%)	4	(21·05%)
Belfast	O	360	103	(28·61%)	239	(66·38%)	18	(5·00%)
	A	182	45	(24·72%)	110	(60·43%)	27	(14·83%)
	B	79	18	(22·78%)	56	(70·88%)	5	(6·32%)
	AB	23	7	(30·43%)	16	(69·56%)	0	
Dublin	O	329	87	(26·44%)	221	(67·17%)	21	(6·38%)
	A	182	59	(32·41%)	106	(58·24%)	17	(9·34%)
	B	73	16	(21·91)%	50	(68·49%)	7	(9·58%)
	AB	13	3	(23·07%)	8	(61·53%)	2	(15·38%)
Westray	O	151	53	(35·10%)	94	(62·25%)	4	(2·65%)
	A	119	29	(24·37%)	51	(42·86%)	39	(32·77%)
	B	64	24	(37·50%)	23	(35·94%)	17	(26·56%)
	AB	18	5	(27·78%)	3	(16·66%)	10	(55·56%)

samples from Westray) we have 93 Le (a – b –) secretors and 30 Le (a – b –) non-secretors. We expect 86·5 secretors and 36·5 non-secretors. These expected figures are based on the frequencies of secretors and non-secretors found in the Le (a + b –) and Le (a – b +) phenotypes. The observed figures do not differ significantly from the expected ($\chi^2 = 1 \cdot 65$ $p = 0 \cdot 2$). Thus these secretor/non-secretor frequencies in the Le (a – b –) phenotype are in agreement with the independent inheritance of the Lewis and secretor genes.

TABLE 4. Secretor/non-secretor frequencies in the Le (a–b–) phenotype

	Le (a–b–)	
Centre	Non-secretor	Secretor
London	2	28
Aberdeen	6	23
Belfast	10	29
Dublin	12	13
Total	30 (24·39%)	93 (75·61%)

In conclusion, since secretor genes have been implicated in a number of blood group and disease associations it is important that the significant variation in frequency of these genes between different parts of the British Isles is noted and the appropriate controls selected for comparison, when blood group secretion studies in relation to certain diseases are carried out.

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GENE FREQUENCIES FROM FAMILY DATA

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Introduction

Studies of gene frequencies in populations, whether in relation to their geographical location or to a particular disease group, are usually based on data from random samples of the population under investigation. Many genetics laboratories, however, in Britain and elsewhere possess considerable quantities of information in the form of family data, and this can be utilized to give estimates of gene frequencies and to make comparisons between two or more groups. This may be particularly relevant when the groups are of limited size, as for instance in the case of a rare disease. A method by which this can be done is set out in this paper.

Method

Li (1955) gives a maximum-likelihood (ML) method of estimating gene frequencies using mother–child (or more generally parent–offspring) pairs for the case of 2 alleles without dominance at an autosomal locus. The method is based on the assumptions of random mating and Hardy-Weinberg equilibrium. Such systems as MN, Ss, AK, Hp and PGM may be investigated using this method.

Table 1 shows the genotype frequencies for offspring of all matings, given the above conditions, and Table 2 shows the same frequencies condensed by mother's genotype. p represents the (fractional) frequency of gene A, and the frequency of a is $q=1-p$. If data are collected and arranged in a form equivalent to that of Table 2, Table 3 results; the n_i are observed numbers. If $n=\sum_{i=1}^{7} n_i$ is the total number of mother–child combinations there are 2n individuals with 4n genes. The gene frequencies may be estimated from the n mothers alone or from the n children, but because each child must share a gene with its mother there are only 3n independent genes, and it is not permissible to pool the mothers and children to provide an estimate using both. It is however desirable to use all the data available and the correct procedure is to apply the maximum-likelihood technique to the 7 cells of the table. The log-likelihood L is given by

TABLE 1. Frequency of genotype of offspring for all possible matings in a random mating population with a 2 gene system in Hardy-Weinberg equilibrium

Mating ♀	Mating ♂	Frequency of mating	Genotype of offspring AA	Aa	aa
AA	AA	p^4	p^4		
AA	Aa	$2p^3q$	p^3q	p^3q	
AA	aa	p^2q^2		p^2q^2	
Aa	AA	$2p^3q$	p^3q	p^3q	
Aa	Aa	$4p^2q^2$	p^2q^2	$2p^2q^2$	p^2q^2
Aa	aa	$2pq^3$		pq^3	pq^3
aa	AA	p^2q^2		p^2q^2	
aa	Aa	$2pq^3$		pq^3	pq^3
aa	aa	q^4			q^4

$$L=n_1 \log p^3+(n_2+n_3)\log p^2q+n_4 \log pq+(n_5+n_6)\log pq^2+n_7 \log q^3.$$

Collecting terms,

$$L=B \log p+C \log q$$

where

$$B=3n_1+2(n_2+n_3)+n_4+(n_5+n_6)$$

and

$$C=(n_2+n_3)+n_4+2(n_5+n_6)+3n_7.$$

The maximum-likelihood equation is $\frac{dL}{dp}=0$

and, remembering that $q=1-p$, it may be solved for p, giving

$$p=\frac{B}{B+C}.$$

TABLE 2. Frequency of genotype of offspring for all possible maternal genotypes in a random mating population with a 2 gene system in Hardy-Weinberg equilibrium.

		Child		
		AA	Aa	aa
Mother	AA	p^3	p^2q	
	Aa	p^2q	pq	pq^2
	aa		pq^2	q^3

TABLE 3. Observed frequencies of mother-child genotype combinations.

		Child		
		AA	Aa	aa
Mother	AA	n_1	n_2	
	Aa	n_3	n_4	n_5
	aa		n_6	n_7

The ML equations may be derived in a similar fashion for any number of alleles, with or without dominance. In the case of 2 genes with dominance the ML equation for the gene frequency estimate may be reduced to a cubic. For more than 2 alleles the equations may be solved using matrix algebra. An iterative method of solution is used, which employs the information matrix M given by

$$M_{ij}=-\frac{\partial^2 L}{\partial p_i \partial p_j}.$$

Starting from an approximation $\mathbf{p}^{(0)}$ to the set of gene frequencies $\mathbf{p}=(p_1, p_2, \ldots p_{k-1})$, for a k-allelic locus a better approximation

$\mathbf{p}^{(1)}$ is found by

$$\mathbf{p}^{(1)}=\mathbf{p}^{(0)}+\left[\mathrm{M}^{-1}\frac{\partial \mathrm{L}}{\partial p}\right]_{p^{(0)}}$$

The process is repeated until 2 successive approximations agree sufficiently closely. The variance–covariance matrix for the gene-frequency estimates and the expected numbers of each mother–child combination are readily found, in addition to the gene-frequency estimates themselves.

A computer program which performs the analysis for any of the 2 or 3 gene cases has been written (in APL for use on an IBM 360/67) and used to provide the results which follow.

Results

To illustrate the usefulness of the method preliminary data for blood groups and isoenzymes from a series of families in which juvenile peptic ulcer is present were examined by the method outlined above, and the gene frequencies were compared with a series of control families. The material was made available by courtesy of our colleagues Dr. R. H. Jackson and Dr. W. M. Cowan.

The MN groups were treated as a 2-gene system without dominance; the Rhesus (D) positive and negative as a 2-gene system with dominance; the acid phosphatase types as a 3-gene system without dominance; and the ABO blood groups as a 3-gene system with dominance. Table 4 gives a summary of the results obtained. The deficiency of ABO gene A in the peptic ulcer series is significant at the 5 per cent level.

Table 5 gives a summary of the results obtained from an analysis of the children's data alone. No significant differences were detected between the two series. In no case was there a significant difference between the gene frequencies estimated from the children and those estimated from the mother–child pairs, but the smaller standard errors (reduced by a factor of about 0·8)which result from using the larger sample provide the method with its additional power. This is achieved at little extra cost as the use of mother–child pairs is a most convenient way of increasing the size of a sample.

Since the maximum-likelihood method used for gene-frequency estimation depends on the assumption of Hardy–Weinberg equilibrium, the method of Smith (1970) was used when dominance was

TABLE 4. Gene frequency estimates for peptic ulcer and control populations using mother-child data for 4 genetic system (2 and 3 genes with and without dominance); with sample sizes, standard errors and the probabilities that observed differences are due to chance.

Gene		Disease group			Controls			Difference	
		Sample size	Gene frequency	Standard error	Sample size	Gene frequency	Standard error	Normal deviate	Probability
ABO	A	48	0·172	0·033	47	0·277	0·042	1·97	$p<0\cdot05$
	B	48	0·081	0·023	47	0·051	0·019	1·01	n.s.
	O	48	0·747	0·038	47	0·672	0·043	1·31	n.s.
Rh	(D)	48	0·605	0·053	47	0·538	0·052	0·90	n.s.
MN		48	0·537	0·043	47	0·444	0·046	1·48	n.s.
AcPh	A	33	0·392	0·051	32	0·263	0·047	1·86	n.s.
	B	33	0·566	0·052	32	0·672	0·050	1·47	n.s.
	C	33	0·042	0·021	32	0·065	0·026	0·69	n.s.

TABLE 5. Gene frequency estimates for peptic ulcer and control populations using data for children only for 4 genetic system (2 and 3 genes with and without dominance); with sample sizes, standard errors and the probabilities that observed differences are due to chance.

Gene		Disease group			Controls			Difference	
		Sample size	Gene frequency	Standard error	Sample size	Gene frequency	Standard error	Normal deviate	Probability
ABO	A	48	0·183	0·042	47	0·272	0·050	1·36	not significant
	B	48	0·075	0·027	47	0·055	0·024	0·55	
	O	48	0·742	0·047	47	0·674	0·052	0·97	
Rh	(D)	48	0·592	0·066	47	0·516	0·064	0·83	
MN		48	0·552	0·051	47	0·468	0·051	1·16	
AcPh	A	33	0·409	0·061	32	0·266	0·055	1·74	
	B	33	0·530	0·061	32	0·656	0·059	1·48	
	C	33	0·061	0·029	32	0·078	0·034	0·38	

absent to test for significant deviations from that situation. None were found.

Summary

The use of mother–child pairs provides a sensitive method for estimating gene frequencies and is particularly useful where data are limited. The method is illustrated by a comparison of isoenzyme gene frequencies between a series of families with juvenile peptic ulcer and a control series.

Acknowledgements

Thanks are due to Dr. R. H. Jackson and Dr. W. M. Cowan for making available the data on which this study is based, and to Dr. D. F. Roberts who suggested this approach.

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Appendix

The authors will be happy to process any parent–offspring data sent to them. The computer program requires data in one of the following forms.

I. 2 genes without dominance.

		Child		
		AA	Aa	aa
Mother	AA	x	x	
	Aa	x	x	x
	aa		x	x

II. 2 genes with dominance.

		Child	
		Dom	Rec
Mother	Dom	x	x
	Rec	x	x

III. 3 genes without dominance.

		Child					
		CC	CA	AA	CB	BB	AB
Mother	CC	x	x		x		
	CA	x	x	x	x		x
	AA		x	x			x
	CB	x	x		x	x	x
	BB				x	x	x
	AB		x	x	x	x	x

IV. 3 genes with dominance.

		Child			
		O	A	B	AB
Mother	O	x	x	x	
	A	x	x	x	x
	B	x	x	x	x
	AB		x	x	x

SKIN COLOUR IN NORTHUMBERLAND

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As the first part of a project (supported by the Wenner-Gren Foundation and the University of Arizona), designed to explore the frequently assumed but not yet quantified relationship between skin colour and climate, 337 Northumbrian school children were examined during the autumn of 1971. The sample consisted of 166 boys and 171 girls, aged 15 and 16, attending 13 secondary schools scattered throughout Northumberland. Reflectance measurements were determined at nine separate wavelengths, by an EEL spectrophotometer. The inner surface of the upper right arm was the spot chosen for study. The results were recorded by Leonie Hulse. The selection of schools to be visited was made by Dr. D. F. Roberts, in consultation with Dr. Hurley of the County Education Office, in such a manner as to insure that different sections of the county were represented. Thus intracounty variations, if any exist, might be ascertained and compared. Figure 1 indicates the geographical distribution of the schools which participated. Parental permission was obtained, in writing, for each child observed, before each school was visited, and on the same forms the parents also kindly provided information concerning the birthplace of the children, their parents, and their grandparents.

Results

It frankly surprised me as a visitor to discover how much population movement has taken place, during the past two generations, within Britain. Of 166 boys and 171 girls, respectively only 95 and 107 (60 per cent) had all four grandparents born in the English

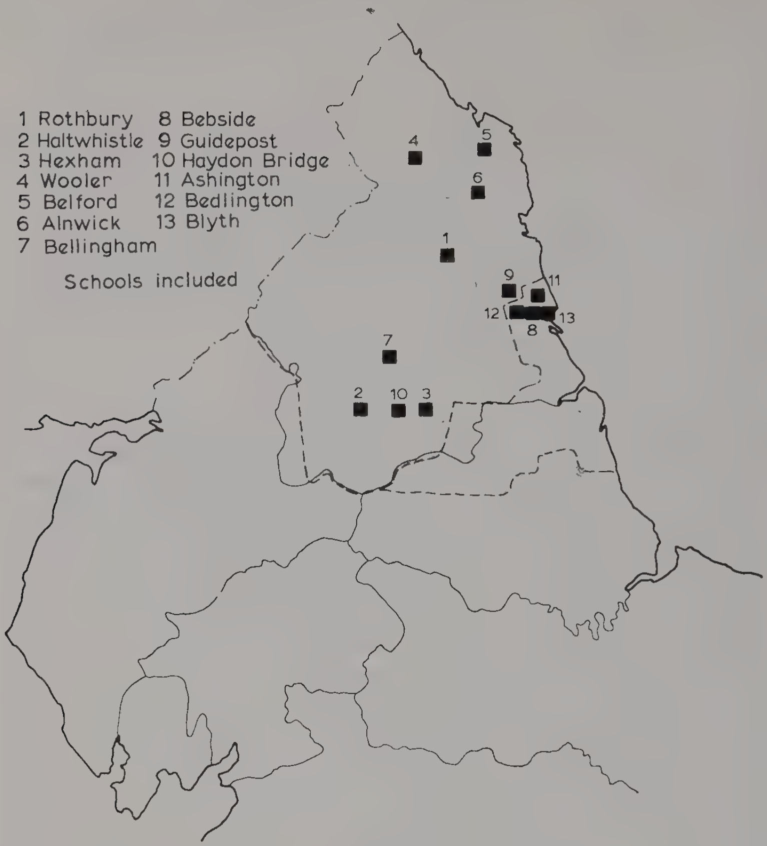

FIG. 1

border counties, and few children attend schools near their grandparents' birthplaces. Rural Northumberland seems to have been at least as much affected as the coal-mining areas, but little migration between the two was revealed. This should be taken into account in considering the results of the survey.

The means and standard deviations for each school at each of the nine wavelengths used are set out by sex in Table 1, together with the results for the total sample. The high percentage reflectance is very noticeable and is consistent over all schools. No differences could be found between the 15 year old and the 16 year old youngsters, so that they are grouped together throughout. Comparison is made

TABLE 1. Reflectance by school and sex—entire population

School	Filter 1		Filter 2		Filter 3		Filter 4		Filter 5		Filter 6		Filter 7		Filter 8		Filter 9		
	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	no.
Male																			
Rothbury	34·67	5·51	41·67	6·51	43·00	4·58	49·00	2·65	48·00	2·65	50·00	2·65	60·33	2·52	64·68	3·06	67·68	2·52	3
Haltwhistle	33·31	3·59	39·23	4·38	44·23	3·70	45·15	3·29	45·39	2·47	50·69	3·61	59·51	3·98	65·54	3·62	68·15	3·56	13
Hexham	37·27	5·99	45·73	7·40	48·27	6·70	47·64	5·71	45·55	5·72	50·27	6·07	61·00	6·87	69·00	6·83	70·36	5·84	11
Wooler	32·81	4·20	38·88	3·96	43·75	4·58	43·88	4·15	43·75	2·79	48·31	3·09	56·63	2·96	64·13	3·01	67·19	3·02	16
Belford	31·38	3·20	35·75	2·87	40·00	4·28	42·63	4·53	42·00	2·14	46·50	1·85	56·63	2·45	65·00	2·14	67·75	2·19	8
Alnwick	30·75	3·77	36·13	3·14	40·50	3·16	43·63	2·93	42·13	1·89	47·25	1·75	55·75	2·96	64·13	3·23	67·38	3·07	8
Bellingham	30·90	5·90	34·40	4·97	38·00	5·01	41·20	5·45	40·00	3·68	46·20	3·65	55·60	3·66	63·70	3·95	66·50	4·12	10
Bebside	28·11	3·30	33·67	4·00	38·22	4·49	40·33	4·30	39·33	3·12	44·56	2·07	52·56	3·32	61·44	3·71	63·89	4·20	9
Guidepost	32·09	4·06	38·00	3·29	41·18	3·52	41·82	4·26	40·55	3·01	45·82	3·74	54·91	2·55	63·64	2·54	66·36	2·34	11
Haydon Bridge	35·00	4·56	41·22	5·02	45·00	4·75	45·35	4·28	43·66	3·54	48·13	3·71	59·65	4·57	66·74	4·14	69·22	3·52	23
Ashington	36·21	5·64	42·71	6·59	46·11	6·27	46·89	5·42	44·50	4·77	49·32	5·03	60·11	5·14	67·18	5·15	69·36	4·55	28
Bedlington	31·71	4·28	36·82	4·42	40·77	5·19	42·53	4·77	40·41	4·11	46·77	3·73	55·94	4·01	63·29	4·21	66·18	3·99	17
Blyth	36·44	4·03	40·56	3·47	44·89	3·52	46·33	3·24	43·56	2·51	49·78	3·07	58·78	2·99	65·89	2·85	68·22	3·38	9
Total	33·55	5·12	39·37	5·80	43·25	5·61	44·46	4·93	42·98	4·12	48·09	4·11	57·80	4·66	65·30	4·43	67·84	4·03	166
Female																			
Rothbury	39·00	3·80	44·73	5·33	49·36	5·09	49·73	6·57	49·27	4·47	54·91	4·87	63·36	4·93	69·00	3·49	71·09	2·88	11
Haltwhistle	41·27	3·95	46·82	5·23	51·18	4·02	51·55	4·37	50·82	4·14	55·91	3·59	64·46	4·23	70·82	3·25	73·36	2·62	11
Hexham	36·64	4·23	42·41	4·60	44·68	4·68	45·09	3·83	43·09	3·75	47·32	3·73	58·50	4·14	66·09	3·05	68·59	2·81	22
Wooler	35·25	4·57	40·50	5·07	45·00	4·08	45·75	5·56	42·50	3·79	50·25	3·30	59·50	2·89	65·00	4·08	67·25	2·99	4
Belford	32·17	5·42	38·33	5·24	42·50	4·85	44·00	3·90	42·00	3·03	48·67	3·14	55·83	3·13	65·33	3·56	68·17	3·37	6
Alnwick	35·00	3·96	39·22	3·93	44·11	4·01	45·28	3·89	43·11	3·50	48·94	4·58	56·89	3·82	64·78	2·44	67·56	2·26	18
Bellingham	33·00	3·63	38·08	4·37	42·08	4·29	43·54	3·69	42·23	2·92	48·15	2·85	56·31	3·79	63·39	4·66	66·77	3·30	13
Bebside	37·14	2·61	41·86	3·72	46·57	3·78	47·29	2·75	45·57	2·23	51·00	2·16	59·43	2·76	65·29	2·29	67·71	1·98	7
Guidepost	35·18	3·57	41·09	4·06	43·91	3·33	43·00	3·07	42·64	2·94	46·36	2·66	57·82	2·75	63·91	2·30	65·82	2·09	11
Haydon Bridge	36·61	5·46	43·13	6·16	46·52	6·61	46·48	5·11	44·97	4·42	49·81	4·06	60·90	3·99	67·48	3·84	69·00	3·62	31
Ashington	37·13	2·53	44·25	1·91	46·38	2·45	46·38	2·51	45·00	4·07	50·25	3·45	62·38	2·39	69·63	3·07	70·63	3·11	8
Bedlington	35·54	4·49	40·50	4·37	44·23	4·43	45·85	4·12	43·96	3·22	49·19	3·43	58·85	3·38	66·50	3·76	69·00	3·64	26
Blyth	29·33	3·06	34·33	3·51	39·00	4·00	41·67	4·04	39·33	2·52	45·00	2·65	53·33	2·08	59·33	3·51	62·33	3·06	3
Total	36·10	4·70	41·67	5·25	45·35	5·22	46·01	4·69	44·44	4·33	49·63	4·40	59·36	4·39	66·37	3·98	68·67	3·55	171

in Table 2 with the few other samples from the United Kingdom and from northwest Europe. Fairness indeed appears to be a Northumbrian characteristic, though this may be due in part to the fact that the northwest European and English samples represent an older age group. The higher Northumbrian reflectance is particularly apparent at wavelengths 545 to 685 mμ, while there is much less difference from the other English samples at wavelengths 425 to 515 mμ. (Fig. 2). The Northumberland male data resemble more the samples from Mainz and Brussels at the higher wavelengths and are appreciably darker at wavelengths 425 to 515 mμ. The Northumberland female data show somewhat higher reflectance than the Belgian at the higher wavelengths, slightly lower at the lower.

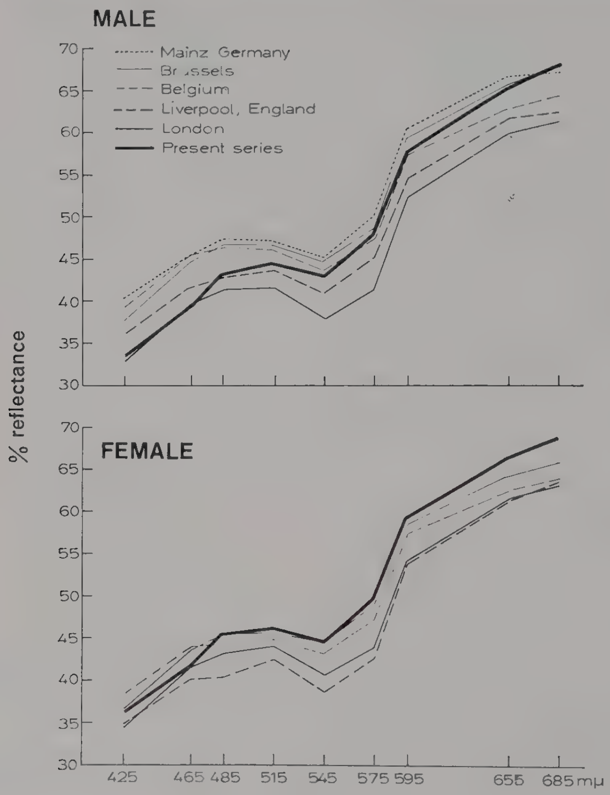

FIG. 2

TABLE 2. European comparative data

				Filter									
Sample	Locality	Sex	No.	601	602	603	604	605	606	607	608	609	Ref.
German	Mainz	M	70	40·3	45·5	47·4	47·1	45·2	50·1	60·6	66·7	66·9	1
Belgian	Brussels	M	143	37·71	44·73	46·74	46·71	44·77	48·87	59·52	65·72	67·27	2
		F	177	36·50	43·48	45·31	45·65	44·57	48·77	58·50	64·28	65·88	
Belgian	Belgium	M	69	39·12	45·54	46·58	46·13	43·80	47·49	57·36	62·86	64·51	3
		F	46	38·81	43·70	44·48	44·80	43·15	47·20	57·28	62·59	63·65	
European	England	F	23	34·93	40·04	41·30	42·34	38·58	42·63	53·78	61·22	62·97	4
European	Liverpool	M & F	>45	36·1	41·6	43·0	43·7	41·0	45·2	54·8	61·7	62·30	5
English	London	M	50	32·8	39·7	41·4	41·6	37·9	41·4	52·4	59·9	61·50	6
		F	50	34·3	41·4	43·1	43·9	40·5	43·9	54·3	61·5	63·10	
Present series													
English	Northumberland	M	166	33·55	39·37	43·25	44·46	42·98	48·09	57·80	65·30	67·84	
		F	171	36·10	41·67	45·35	46·01	44·44	49·63	59·36	66·37	68·67	

References 1. Ojikutu (1965). 2. Leguebe (1961). 3. Tournel (1965). 4. Tiwari (1963). 5. Harrison & Owen (1964). 6. Barnicot (1958).

The correlations between readings at different filters on the total sample are set out in Table 3 for each sex. It appears that there is a general tendency for readings to be more highly correlated with each other the closer the wavelength. There may well be a slight reduction in males in the correlations particularly of filter 5 with filters 1 and 2, which does not appear in females. However the correlation coefficients are not so high as to suggest that readings at one or two filters would adequately replace readings at all nine.

The data were broken down by the locality of birth of the child, using the same localities as those employed by Kopeć (1970). Twenty such localities within the counties of Northumberland and Durham were represented in the sample, so that in the majority there

TABLE 3. Correlations between reflectance readings at nine wavelengths

Total sample					Filter				
	1	2	3	4	5	6	7	8	9
1	1·000	0·934	0·832	0·757	0·737	0·738	0·738	0·723	0·700
2		1·000	0·879	0·766	0·750	0·763	0·778	0·778	0·736
3			1·000	0·809	0·805	0·801	0·828	0·815	0·788
4				1·000	0·919	0·871	0·832	0·759	0·769
5					1·000	0·907	0·868	0·827	0·820
6						1·000	0·915	0·866	0·861
7							1·000	0·931	0·899
8								1·000	0·922
9									1·000
Males									
1	1·000	0·944	0·864	0·755	0·719	0·730	0·750	0·737	0·718
2		1·000	0·903	0·761	0·728	0·756	0·794	0·799	0·762
3			1·000	0·822	0·773	0·792	0·828	0·828	0·807
4				1·000	0·915	0·856	0·833	0·785	0·802
5					1·000	0·900	0·857	0·818	0·810
6						1·000	0·921	0·874	0·870
7							1·000	0·941	0·905
8								1·000	0·913
9									1·000
Females									
1	1·000	0·919	0·794	0·760	0·755	0·740	0·718	0·700	0·677
2		1·000	0·848	0·769	0·767	0·762	0·750	0·746	0·699
3			1·000	0·787	0·826	0·799	0·815	0·788	0·754
4				1·000	0·919	0·880	0·823	0·721	0·723
5					1·000	0·912	0·873	0·829	0·824
6						1·000	0·904	0·849	0·848
7							1·000	0·913	0·885
8								1·000	0·925
9									1·000

were few subjects of each sex (Table 4). Six children were born in the Scottish border counties, and twenty-five outside the border area. Inspection of the means suggests a tendency for natives of rural Northumberland, as distinct from those of the industrialized south and east of the county, to be characterized by rather higher mean reflectance values. For example of the six localities from rural Northumberland represented by a male sample of more than one individual, four had a mean value at filter 9 of 68·5 or above, while none of the four from the industrial southeast part of the county had a mean greater than 67·5.

The localities of birth were therefore grouped into regions. Kopeć (1970) showed that the English border counties were not homogeneous in their ABO blood group frequencies, and distinguished four areas, within each of which frequencies were quite uniform, but between which significant differences occurred. These blood group areas were taken as the basis of subdivision of the present sample. From the design of the investigation almost all subjects came from two areas. Ninety three boys and 104 girls from rural Northumberland (Kopeć's 1st area) and 55 boys and 51 girls from southeast Northumberland (her 2nd area). Only two boys and one girl had been born in her third area (central County Durham) and one in her fourth (Cumberland, North Westmorland, and southwest Durham). For purposes of this analysis the six children from the adjoining Scottish counties were assigned a separate area, and so were the children born outside the region. Analysis of variance within and between sexes, and between and within areas within sexes, showed a significant difference between sexes at all filters, highly significant at filters 1 to 7. Differences between areas within sexes are significant at filters 4 to 9, and highly so at filters 6 and 9 (Table 5). Examining in more detail the two Northumberland samples, the means and standard deviations are given in Table 6. In both boys and girls the mean reflectance at each filter is consistently lower in area two than it is in area one. This is the case not only when the total samples are considered, but also when only those children are included who had four grandparents born in the English border counties (Fig. 3). For the total sample these differences are significant in males at filters 5 to 9, highly so at filters 7 and 9, and in the rather smaller samples of boys with four local grandparents they remain significant at filters 5, 6, 8 and 9. For girls the differences do not reach significance, but are in the the same direction consistently.

TABLE 4. Analysis by birthplace

Males	Filter 1		Filter 2		Filter 3		Filter 4		Filter 5		Filter 6		Filter 7		Filter 8		Filter 9		
Location	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	No.
Berwick	36·00	5·66	42·00	6·26	44·67	7·01	45·17	5·91	45·83	3·97	49·33	3·67	59·33	5·47	67·00	3·58	69·33	2·50	6
Wooler	35·75	4·50	41·00	4·97	45·00	6·22	46·75	4·99	45·00	3·46	49·75	3·78	57·00	2·94	64·50	2·89	67·50	2·89	4
Seahouses	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Alnwick	32·27	3·88	38·37	3·80	42·82	2·75	44·73	2·37	43·46	2·02	48·73	2·41	57·55	2·73	65·82	3·19	68·82	2·68	11
Morpeth	34·65	6·45	39·97	6·71	43·52	6·94	45·90	5·70	43·79	4·69	49·03	4·18	58·69	5·12	65·83	4·87	68·52	4·47	29
Hexham	34·24	5·30	40·12	6·69	44·29	6·02	45·10	5·00	43·66	4·40	48·93	4·60	59·22	5·37	66·71	5 24	68·88	4·78	41
Newcastle 2	24·00	—	32·00	—	35·00	—	36·00	—	37·00	—	42·00	—	52·00	—	60·00	—	63·00	—	1
Newcastle 7	34·15	3·81	40·31	3·84	44·23	3·83	45·15	3·24	43·54	2·57	48·54	3·60	57·77	3·86	65·23	3·52	67·39	3·64	13
Wallsend	35·00	—	42·00	—	45·00	—	44·00	—	45·00	—	51·00	—	62·00	—	68·00	—	73·00	—	1
Dudley	33·00	—	41·00	—	44·00	—	47·00	—	43·00	—	49·00	—	55·00	—	65·00	—	68·00	—	1
Bedlington	31·10	3·81	36·80	3·65	41·10	4·77	42·40	4·09	40·20	3·39	46·40	2·91	55·10	3·18	62·80	3·85	65·60	3·31	10
Ashington	33·50	4·75	39·79	5·89	43·00	5·52	43·93	5·28	42·29	4·21	47·00	4·08	57·29	4·65	64·64	4·01	67·21	3·36	14
Blyth	33·57	5·02	38·43	5·13	42·57	5·29	44·00	4·77	42·07	3·99	46·50	4·24	56·86	4·57	64·36	4·18	66·43	4·36	14
North Shields	30·33	2·52	38·00	4·00	41·33	3·22	43·67	5·03	40·67	2·08	45·67	2·08	54·67	2·08	63·67	2·08	65·67	1·16	3
Sunderland	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gateshead	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Consett	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Seaham	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Durham	30·00	—	36·00	—	40·00	—	38·00	—	41·00	—	45·00	—	52·00	—	58·00	—	68·00	—	1
Middlesbrough	42·00	—	52·00	—	53·00	—	52·00	—	48·00	—	52·00	—	64·00	—	71·00	—	73·00	—	1
Scottish border Counties	33·67	1·53	36·67	1·16	41·33	2·52	40·33	1·16	41·67	2·08	48·33	2·52	56·33	2·08	65·33	2·52	68·33	1·53	3
Out of this area	31·00	4·53	36·62	5·90	41·00	5·58	41·54	5·03	40·92	4·70	44·92	4·43	59·08	5·63	63·08	3·59	66·00	3·19	13

TABLE 4 *(continued)*

Females	Filter 1		Filter 2		Filter 3		Filter 4		Filter 5		Filter 6		Filter 7		Filter 8		Filter 9		
Location	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	No.
Berwick	37·00	5·66	44·00	5·66	48·00	4·23	48·50	4·95	45·00	4·24	51·50	3·54	59·00	1·14	67·50	2·12	69·50	2·12	2
Wooler	30·50	4·95	35·00	5·66	39·50	4·95	41·00	4·24	39·00	1·41	45·50	3·54	54·50	6·36	63·00	5·66	66·50	4·95	2
Seahouses	31·50	2·12	37·00	1·41	40·50	2·12	45·00	2·83	43·50	3·54	50·50	2·12	57·00	1·41	65·00	1·41	68·50	3·54	2
Alnwick	35·85	3·65	40·15	3·81	44·77	4·21	45·92	4·63	43·69	4·92	49·77	5·00	58·08	4·07	65·69	3·62	68·15	2·80	13
Morpeth	36·83	4·37	42·44	5·04	46·57	5·25	47·26	5·86	46·39	4·60	51·83	5·10	60·96	4·65	67·48	3·29	69·48	3·12	23
Hexham	36·80	5·37	42·80	6·05	46·08	6·20	46·32	5·07	44·72	4·67	49·53	4·46	59·75	4·72	66·67	4·43	68·97	3·95	60
Newcastle 2	36·00	1·41	42·00	1·41	44·50	0·71	45·50	0·71	42·50	0·71	48·50	0·71	60·00	2·83	68·00	2·83	70·50	0·71	2
Newcastle 7	36·13	4·05	42·38	4·69	46·00	2·83	46·63	3·07	44·25	2·12	49·25	1·04	59·28	2·77	66·13	2·70	68·00	2·51	8
Wallsend	30·00	2·83	36·50	2·12	40·00	2·83	42·50	4·95	41·50	0·71	46·50	2·12	57·50	2·12	65·50	2·12	68·00	2·83	2
Dudley	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bedlington	35·15	4·47	40·31	4·29	44·46	4·70	45·77	4·48	44·31	3·52	49·39	4·11	58·92	3·59	66·46	4·03	68·92	3·84	13
Ashington	38·00	3·16	44·50	2·07	46·33	2·66	46·50	2·67	45·00	4·20	49·67	2·94	62·17	2·30	69·67	3·67	71·50	2·07	6
Blyth	35·50	5·45	40·42	5·45	44·58	5·32	45·08	4·56	43·67	4·40	48·75	4·45	58·17	4·02	63·75	4·50	66·42	4·30	12
North Shields	34·60	3·44	40·20	4·60	42·80	5·40	44·20	4·82	42·60	5·37	46·60	4·51	57·40	6·23	65·40	5·13	68·00	4·85	5
Sunderland	41·00	—	46·00	—	49·00	—	49·00	—	47·00	—	52·00	—	61·00	—	64·00	—	67·00	—	1
Gateshead	36·00	1·73	40·00	2·00	43·00	1·00	45·33	0·58	42·67	0·58	49·00	3·00	59·33	2·31	65·67	2·08	67·67	2·08	3
Consett	34·00	—	41·00	—	42·00	—	43·00	—	43·00	—	48·00	—	60·00	—	67·00	—	70·00	—	1
Seaham	38·00	—	41·00	—	42·00	—	44·00	—	43·00	—	48·00	—	57·00	—	64·00	—	67·00	—	1
Durham	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Middlesbrough	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scottish border Counties	38·00	3·46	41·67	4·62	46·33	3·51	46·33	2·31	43·00	1·73	48·67	2·08	58·33	0·58	65·00	2·65	67·67	2·89	3
Out of this area	34·50	4·74	40·08	5·93	44·75	5·23	44·92	4·87	44·25	4·94	49·92	5·79	55·62	3·95	66·33	3·96	68·25	3·28	12

TABLE 5. Analysis of variance

	s.o.s.	d.f.	ms.	s.o.s.	d.f.	m.s.	s.o.s.	d.f.	m.s.
	Filter 1			Filter 2			Filter 3		
Between areas within sexes	218·17	4	54·54^{+}	282·94	4	70·74^{+}	220·01	4	55·00^{+}
Within areas within sexes	7858·27	331	23·74^{+}	9959·75	331	30·09^{+}	9593·61	331	28·98^{+}
Within sexes	8076·44	335	24·11$^{\times}$	10242·69	335	30·58$^{\times}$	9813·63	335	29·29$^{\times}$
Between sexes	545·56	1	545·56$^{\times}$	445·19	1	445·19$^{\times}$	370·69	1	370·69$^{\times}$
Total	8622·00	336		10687·88	336		10184·31	336	
	$^{+}$F=2·297			$^{+}$F=2·351			$^{+}$F=1·897		
	$^{\times}$F=22·610**			$^{\times}$F=14·560**			$^{\times}$F=12·654**		
	Filter 4			Filter 5			Filter 6		
Between areas within sexes	287·11	4	71·78^{+}	208·21	4	52·05^{+}	276·10	4	69·03^{+}
Within areas within sexes	7459·32	331	22·54^{+}	5776·91	331	17·45^{+}	5797·40	331	17·52^{+}
Within sexes	7746·44	335	23·12$^{\times}$	5985·13	335	17·87$^{\times}$	6073·5	335	18·13$^{\times}$
Between sexes	200·13	1	200·13$^{\times}$	178·69	1	178·69$^{\times}$	200·75	1	200·75$^{\times}$
Total	7946·56	336		6163·81	336		6274·25	336	
	$^{+}$F=3·185*			$^{+}$F=2·983*			$^{+}$F=3·941**		
	$^{\times}$F=8·654**			$^{\times}$F=9·996**			$^{\times}$F=11·073**		
	Filter 7			Filter 8			Filter 9		
Between areas within sexes	241·43	4	60·36^{+}	210·14	4	52·54^{+}	199·02	4	49·75^{+}
Within areas within sexes	6627·19	331	20·02^{+}	5708·55	331	17·25^{+}	4620·67	331	13·96^{+}
Within sexes	6868·63	335	20·50$^{\times}$	5918·69	335	17·67$^{\times}$	4819·69	335	14·39$^{\times}$
Between sexes	207·38	1	207·38$^{\times}$	99·31	1	99·31$^{\times}$	59·31	1	59·31$^{\times}$
Total	7076·00	336		6018·00	336		4879·00	336	
	$^{+}$F=3·015*			$^{+}$F=3·046*			$^{+}$F=3·564**		
	$^{\times}$F=10·114**			$^{\times}$F=5·621*			$^{\times}$F=4·123*		

* = sig. at 0·05. ** = sig. at 0·01.

TABLE 6. Comparison of reflectance by Northumberland regions

Place of birth of child	Filter 1		Filter 2		Filter 3		Filter 4		Filter 5		Filter 6		Filter 7		Filter 8		Filter 9		
	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	m	S.D.	No.
Total sample																			
Male																			
N. Northumberland	34·17	5·56	40·01	6·25	43·78	6·04	45·30	5·03	43·81	4·20	48·91	4·11	58·69	4·91	66·16	4·69	68·63	4·24	93
S.E. Northumberland	33·02	4·32	38·91	4·70	42·71	4·72	43·95	4·37	42·09	3·61	47·40	3·71	56·76	4·11	64·38	3·79	66·82	3·65	55
	$t=1\cdot32$		$t=1\cdot13$		$t=1\cdot13$		$t=1\cdot66$		$t=2\cdot53$*		$t=2\cdot10$*		$t=2\cdot77$**		$t=2\cdot39$*		$t=2\cdot65$**		
Female																			
N. Northumberland	36·45	4·91	42·14	5·58	45·80	5·67	46·38	5·09	44·79	4·66	50·03	4·64	59·64	4·60	66·66	4·02	68·93	3·56	104
S.E. Northumberland	35·61	4·32	41·10	4·45	44·57	4·29	45·53	3·88	43·88	3·59	48·86	3·56	59·08	3·73	65·92	4·02	68·28	3·67	51
	$t=1\cdot05$		$t=1\cdot28$		$t=1\cdot38$		$t=1\cdot05$		$t=1\cdot22$		$t=1\cdot58$		$t=0\cdot76$		$t=1\cdot08$		$t=1\cdot06$		
Children with four northern grandparents																			
Male																			
N.Northumberland	34·26	5·06	39·90	5·70	43·93	5·55	45·60	4·52	44·09	3·94	49·26	3·97	58·83	4·55	66·38	4·37	68·97	3·89	58
S.E. Northumberland	33·46	4·43	39·24	4·51	42·92	4·75	44·22	4·42	42·27	3·64	47·62	3·71	57·08	4·37	64·46	4·07	66·95	3·93	37
	$t=0\cdot79$		$t=0\cdot59$		$t=0\cdot92$		$t=1\cdot47$		$t=2\cdot25$*		$t=2\cdot01$*		$t=1\cdot85$		$t=2\cdot14$*		$t=2\cdot46$*		
Female																			
N. Northumberland	37·12	4·46	42·79	5·01	46·37	5·33	46·90	4·49	45·30	4·45	50·55	4·26	59·97	4·28	66·94	3·81	69·33	3·17	67
S.E. Northumberland	36·55	3·82	42·13	4·02	45·38	4·02	46·00	3·78	44·40	3·57	49·23	3·54	59·68	3·50	66·50	3·74	68·70	3·39	40
	$t=0\cdot67$		$t=0\cdot71$		$t=1\cdot02$		$t=1\cdot06$		$t=1\cdot09$		$t=1\cdot66$		$t=0\cdot37$		$t=0\cdot58$		$t=0\cdot97$		

* significant at 0·05. ** significant at 0·01.

It appears therefore that between rural Northumberland (i.e. the greater part of the county), and southeast Northumberland, there occur differences in skin pigmentation. Though there may be other interpretations, it seems reasonable to suggest that these may be of genetic origin, paralleling the differences in allele frequency between the two areas that the study of monogenic characters, particularly the ABO blood groups, indicated. What the sources of such genetic differences may be we cannot say; selection in situ, stimulated by smog, and immigration of miners from elsewhere may be suggested with equal plausibility and equal lack of proof.

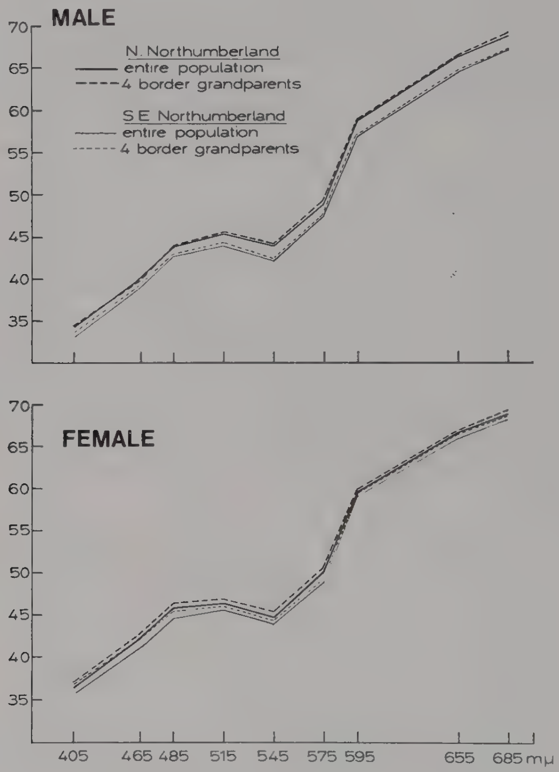

FIG. 3

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SKIN COLOUR STUDIES IN SOUTH WALES, THE ISLE OF MAN AND CUMBRIA

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THIS paper is concerned with skin colour variation found among secondary schoolchildren in Cumberland, the Isle of Man and the Merthyr Tydfil area of South Wales. The data from Merthyr were collected by Joan Smith when obtaining dermatoglyphic data from that area, and the data from Cumberland and the Isle of Man were collected by John Mitchell. Thanks are due to undergraduates of the University of Durham for their assistance in all three areas.

A portable EEL (Evans) reflectance spectrophotometer was used in this study. The instrument is fitted with nine different filters which sample the whole visible spectrum, recording the percentage of light reflected from a surface, relative to the reflectance from a standard white surface, in this case a magnesium carbonate block. In this study readings were taken from the inner aspect of the upper arm and filters 601, 605 and 609 (425 mμ, 545 mμ and 685 mμ wavelengths) were selected.

Human skin colour is mainly due to the presence of four pigments, haemoglobin, carotene, melanin and melanoid, though the colour produced by the scattering of incident light from the skin is also involved. It has been shown, however, that it is variation in the amount of melanin which is mainly responsible for differences in human skin colour. It has also been shown that the measurement of the reflectance at 685 mμ provides the most reliable method of determining the melanin concentrations in skin and consequently for understanding the genetics of skin colour inheritance and its

TABLE 1. Variation in skin colour readings in Cumberland, the Isle of Man and Merthyr Tydfil

		Filter								
		601			605			609		
Area		Males	Females	Total	Males	Females	Total	Males	Females	Total
Cumberland	*n*	99	153	252	99	153	252	99	153	252
	mean	35·78	36·94	36·48	41·80	42·35	42·13	66·46	66·96	66·77
	SD	4·03	4·79	4·57	3·62	4·11	3·92	3·16	2·87	2·99
Isle of Man	*n*	90	73	163	90	73	163	90	73	163
	mean	36·62	36·75	36·68	41·94	41·79	41·88	65·91	67·01	66·41
	SD	4·13	4·4	4·09	3·76	3·58	3·67	2·90	2·69	2·84
Merthyr Tydfil	*n*	84	98	182	84	98	182	84	98	182
	mean	32·77	33·23	33·01	38·71	38·66	38·68	62·80	63·46	63·16
	SD	4·91	3·51	4·31	5·14	3·50	4·36	5·74	3·97	4·85

variability. This is because the haemoglobin contribution to colour affects the reflectance values least at this wavelength.

Analysis of Data

Once the data had been collected, children with fewer than three locally born grandparents were excluded from each regional sample. This was done in an endeavour to relate the skin colour to the indigenous populations and also to standardize comparisons between the areas. This left three samples comprising 252 individuals (99 male and 153 female) from Cumberland; 163 (90 male and 73 female) from the Isle of Man; and 182 (84 male and 98 female) from Merthyr Tydfil. It was felt that the regional samples were large enough to be profitably used for statistical analysis (Table 1).

Each sample was first examined for variation between sexes. The means and standard deviations were calculated for males and females and the statistical significance of the differences examined. The slight sex differences were not found to be significant at any of the three wavelengths. The readings do suggest, however, that, on the whole, males have slightly darker skin than females, in keeping with the results of many previous studies and probably attributable to the fact that males have a richer blood supply to their skin and also tend to expose themselves more to sunlight.

Having found no statistical variation of importance between the sexes, these were then combined into regional samples and inter-regional comparisons conducted at all three wavelengths. Once again, means and standard deviations were calculated (Table 2). It was found that the Cumberland and the Isle of Man samples did not differ statistically from each other but that each differed significantly from the Merthyr Tydfil samples, with the greatest difference occurring between Cumberland and Merthyr Tydfil. The latter population is darker than either of the other two.

Explanation of Differences

It is felt that these inter-regional differences can best be explained in an historical context.

The influences that have acted upon the areas of Cumbria and the Isle of Man have been very similar for a large part of their history.

TABLE 2. Interregional variation

Area		EEL Spectrophotometer filter		
		601	605	609
Cumberland	*n*	252	252	252
	mean reflectance (%)	36·48	42·13	66·77
	SD	4·57	3·92	2·99
Isle of Man	*n*	163	163	163
	mean reflectance (%)	36·68	41·88	66·41
	SD	4·09	3·65	2·84
Merthyr Tydfil	*n*	182	182	182
	mean reflectance (%)	33·01	38·68	63·16
	SD	4·31	4·36	4·85

Both areas show evidence of large scale Celtic settlement but only Cumbria was invaded by the Roman armies who constructed a string of forts along its northern and western boundaries. Between the eighth and twelfth centuries both areas underwent intensive Scandinavian settlement and this is demonstrated particularly by the distribution of placenames, for example the frequency of *dale* and *thwaite* in Cumberland, and *by* in the Isle of Man. Many of the surnames also show Scandinavian origins such as Corlett, Corkill and Christian in the Isle of Man and Satterthwaite and Postlethwaite in Cumberland.

Prior to the Industrial Revolution there was relatively little movement of population in both areas, the characteristic feature of each area being small settlements based upon an agricultural or fishing economy or both. The Industrial Revolution saw the development of many of the market towns of Cumberland into urban centres or ports in the early nineteenth century, especially those on the coalfield such as Workington, Whitehaven and Maryport. However, the Industrial Revolution had little or no effect upon the settlement patterns or population sizes in the Isle of Man where the population numbered 40,081 in 1821, 52,469 in 1861, 52,016 in 1911 and 56,248 in 1971.

The development of tourism on the Isle of Man from the second half of the nineteenth century has caused greater growth of the villages, especially Douglas—from a fishing village of a few hundred people at the beginning of the nineteenth century to a town of over 25,000 in 1972.

In sharp contrast to these two areas is the demographic history of the Merthyr Tydfil area. In pre-Roman times Merthyr lay within the tribal boundaries of the Silures, for whom is claimed a non-Celtic heritage, and they were probably related to Iberian tribes of the neolithic invasions. This part of South Wales, removed from the coast and later Roman and Viking incursions, maintained a relatively stable population within an agricultural and pastoral context.

The onset of the Industrial Revolution drastically changed this long-established pattern of continuity. By the beginning of the nineteenth century Merthyr Tydfil had grown from a hamlet into the chief iron town of the area, becoming the largest town in Wales by 1851. This rapid expansion associated at first with iron working and later with the coal industry continued until the beginning of the twentieth century. In the 1851 census we find that of 35,093 persons over the age of 20 living in Merthyr, only 9,120 (about 25 per cent) had been born in the town, and 4,146 (about 12 per cent) in the county of Glamorgan. Some 21,827 (62 per cent) originated outside the county and of these 14,189 (40 per cent) came from the four Welsh counties of Carmarthen, Brecon, Pembroke and Cardigan. 2,330 (7 per cent) were of Irish birth (a fact largely attributable to the potato famines of the 1840's). Thus, it can be seen that although there was a great deal of population movement within the area during the Industrial Revolution much of the influx came from other parts of Wales. Since the early twentieth century and the decline of the coal industry, the movement of population has been in a different direction—away from the area, a fact obviously correlated with economic circumstances. The virtual cessation of immigration meant some stabilisation of population and a marked decline in the introduction of new genetic material.

From these brief outlines of the history of the three areas, it can be seen that the Isle of Man and Cumberland have a common background of Celtic and Scandinavian influence in contrast to the Merthyr Tydfil area which was relatively unaffected by these racial groups. It has also been shown that the main basis of the population in Cumberland and the Isle of Man is long established, while that of Merthyr is of a relatively recent influx dating largely from the Industrial Revolution.

Conclusion

Studies on the skin colour of a sample of the indigenous populations of Cumberland, the Isle of Man and the Merthyr Tydfil area have shown there exists some local variation within the British Isles. The people of the Merthyr Tydfil area were shown to be significantly darker than those from Cumberland or the Isle of Man, the latter two areas being shown to be similar in pigmentation. An attempt has been made to relate these findings to the historical demography of each area.

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SKIN COLOUR IN THE SIKH COMMUNITY IN BRITAIN

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THE Sikhs in Britain represent waves of invited, not invading, immigrants which started in the early 1950's as an aftermath of labour shortage in this country. Although they include members from different castes, they are predominantly Jat Sikhs—quantitatively the biggest, qualitatively perhaps the most burly and sturdy, and in colouration probably amongst the fairest of all Sikhs. Another important feature of the Sikhs in Britain is that they are predominantly from one area of Punjab, Doaba—the fertile tract bounded by Majha to the west and Malwa to the southeast, the three regions being separated by the rivers Ravi and Sutlej. As their restless spirit has driven many to wander the world, so the Sikhs in Britain have come, some directly from Punjab in India, some from Kenya, Tanzania and Uganda, and others from the far east, from Malaysia and Singapore. Caste, locality of origin, and route to this country are some of the factors which may well influence their skin pigmentation.

Although the earlier waves of Sikh immigrants were predominantly village folk, the later entries after the 1962 Immigration Bill represent, to a greater extent, the educated section of the community who came in pursuit of a better future for themselves. While they may have improved their living standards slightly, many have experienced retrogression in occupation. Many with graduate or indeed postgraduate qualifications are to be found working as unskilled labourers. It is a sad commentary that in Britain's factories in areas of immigrant settlement are to be found hard working Sikh and other Asian graduates toiling on shifts by day and night. The majority of the Sikh immigrants inhabit Britain's prime city, London, and the industrial midlands. In the northeast of England, Scotland and the rest of the country, the Sikhs are only a sprinkling amongst the other immigrant groups, mainly Gujarati Indians and Bangladesh and Pakistani Moslems.

As regards the social and biological milieu from which the Sikhs in Britain have come, different schools of religious thought have from time to time imposed on the groups living in India characteristic social systems, giving rise, in biological terms, to various types of population structure. One such system arose in Sikhism, the most recent and modern religious group which began to emerge as a distinct entity some 500 years ago. Its basic philosophy of casteless society meant breaking the strict endogamy of Hindu society and thus biologically the creation of a grand experiment in random breeding. Genetically this meant for the followers of the Sikh faith the creation of a large Mendelian genepool. Generations of panmixia incorporating the former low and high castes would perhaps have given rise to an intermediate pigmentation. However it was not possible to break away completely from the dominating influence of Hinduism, which continued to pervade the fabric of Sikh society, so the evolution of a casteless structure did not proceed very far. Present day Sikhs whether seen in the streets of this country or of their holy town Amritsar, whether colourful in their turbans or drab in their acculturated clean-shaven looks, are still a product of endogamous units of their caste-ridden mother India. Whether the "British Sikhs", the new anglicized generation growing up here, will be able to withstand the temptations of assimilation in the permissive west, and instead retain their distinctive cultural and genetic heritage, remains to be seen. Socially the Sikhs add variety by way of their culture and customs to the British scene. In terms of pigmentation they add to the range of variation already observable in British folk. In short, they add colour to the British way of life both biologically and socially.

Material and Methods

The sample of Sikhs consists of 130 husband/wife pairs and their 325 offspring collected from Southall, Hounslow, Ealing and other London suburbs, and from Birmingham, Coventry and Newcastle upon Tyne. The data were collected using an EEL spectrophotometer. In using this, a number of precautions were necessary. Regular cross checking with some standard is necessary, particularly in view of the difficulties that may be experienced with the filter 601 (wavelength 425 mμ), and here a marked site on the investigator's right upper inner arm was used. Also it is essential to ensure while zeroing that the base of the spectrophotometer head completely touches the surface of the $MgCO_3$ block. Regular scraping of this block to remove dirt is necessary, and since it is subject to wear, crumbling and breaking, it must be changed frequently. Periodic checks were made against drifting of the reading. Readings were taken on the forehead and the medial aspect of the right inner upper arm, although it was with some reluctance that many a young female offered the latter site for examination. The ages of parents ranged from the mid twenties to the late seventies, while the offspring ranged from 2 to 35 years of age.

Results

Figure 1 shows the reflectance curves for male and female adults on the upper inner arm, by comparison with the Northumberland series presented by Professor Hulse. The diminished reflectance at each wavelength in Sikhs is conspicuous, and so is the different shape of the profile. With the absence of the characteristic dip at 545 mμ due to absorption of haemoglobin that occurs in Europeans in general, the overall profile of the Sikhs is much more regular. In the case of the English, the reflectance curve mirrors the absorption and reflectance characteristics of blood and carotene, but amongst the Sikhs the relatively greater melanin content almost obliterates these characteristics. The general trend of increase in reflectance from the blue towards the red end is clear, but there is little sex difference, the slightly greater reflectance in women only being significant at filters 606 and 607.

Figure 2 compares the readings on the upper inner arm with those on the forehead in Sikh family members, mothers, fathers, sons and daughters; the data are set out in Table 1. The sex difference in adults is more conspicuous on the forehead, all differences between mothers and fathers being highly significant. But the differences between sons and daughters are all highly significant both on the forehead and on the upper inner arm. Indeed on the forehead mothers and daughters are both lighter than fathers and sons, while for the upper inner arm the father and son curves are consistently below those of the mother

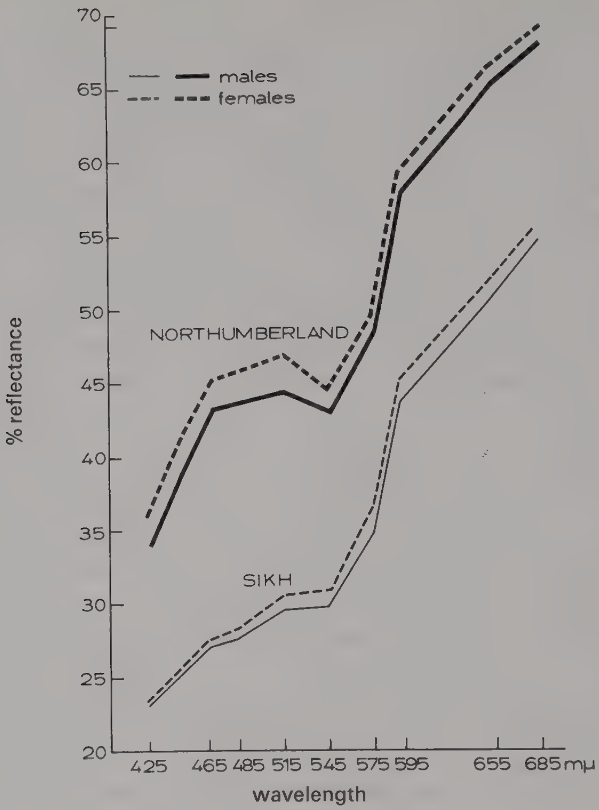

FIG. 1

and daughter respectively. The differences between the relatives are summarized in Table 2, showing the values of *t* for the comparisons. Most non-significant differences occur between mother and daughter on the forehead, and secondly between father and son again on the forehead, though in the latter filters 604–606 show highly significant differences; the forehead differences of mother versus son and of father versus daughter are practically all highly significant. For the upper inner arm all comparisons are highly significant except between father and daughter, where the only highly significant difference occurs at 601. This similarity at greater wavelengths between fathers and daughters probably suggests similarity in melanin concentration, whereas the increasing divergence at the

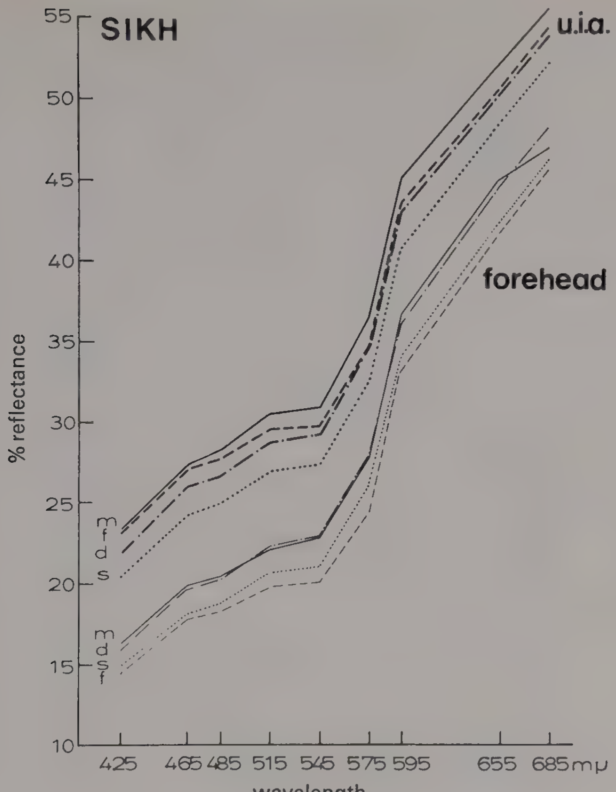

FIG. 2

lower wavelengths suggests probably differences in the content of carotene and the content and flow of blood.

For the upper inner arm sons and daughters have consistently lower reflectance than their parents of the same sex, but this does not occur on the forehead. Moreover Sikh children generally tend to be more variable on their foreheads than their parents of corresponding sex. These differences suggest the existence of an age effect.

The data on the offspring were therefore divided for each sex into four age groups, under 5 years, 5 to 12 years, 13 to 18 years, and over 18 years (Table 3). The sample sizes of the first and last of these are rather small, but there appears a definite trend towards relative darkening from the infant to the preadolescent and adolescent age groups. The smallest children show a tendency to higher mean

TABLE 1. Reflectance readings of family members

	Fathers (130)				Mothers (130)				Sons (173)				Daughters (152)			
	Forehead		U.I.A		Forehead		U.I.A.		Forehead		U.I.A.		Forehead		U.I.A.	
Filter	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
601	14·41	2·38	23·09	3·76	16·29	2·62	23·37	3·35	14·92	2·73	20·54	3·73	15·94	3·87	21·84	3·18
602	17·73	2·62	27·01	4·03	19·82	2·74	27·45	3·70	18·29	3·34	24·21	3·71	19·67	4·47	25·95	3·62
603	18·25	2·86	27·65	4·14	20·28	3·34	28·28	3·98	18·84	3·49	24·98	3·75	20·33	4·64	26·65	3·79
604	19·73	2·63	29·49	4·01	22·21	2·76	30·48	4·07	20·70	3·54	26·96	3·83	22·34	4·73	28·74	3·82
605	20·06	2·70	29·68	3·98	22·81	2·93	30·86	4·02	21·29	3·46	27·42	3·66	22·94	4·53	29·33	3·72
606	24·41	2·96	34·77	4·21	27·78	3·43	36·45	4·06	26·10	3·64	32·60	3·91	27·84	4·76	34·63	3·88
607	33·07	3·75	43·54	4·71	36·79	3·55	45·25	4·18	34·25	4·13	40·95	4·30	36·24	5·01	43·05	4·76
608	41·68	4·61	50·58	4·46	45·05	4·28	52·03	4·28	42·40	4·66	48·41	4·17	44·61	4·99	50·43	5·13
609	45·69	4·40	54·47	3·89	47·16	4·60	55·60	3·76	46·40	4·34	52·43	3·64	48·38	4·14	54·06	4·67

Table 2. Values of *t* for comparisons between relatives in % reflectance

t Test

	Father v son		Mother v son		Father v daughter		Mother v daughter		Son v daughter	
Filter	Forehead	U.I.A.	Forehead	U.I.A.	Forehead	U.I.A.	Forehead	U.I.A.	Forehead	U.I.A.
601	(1·73)	5·87	4·39	6·82	3·93	3·03	(0·87)	3·92	2·76	3·36
602	(1·58)	6·27	4·26	7·52	4·35	2·33*	(0·32)	3·42	3·18	4·27
603	(1·58)	5·89	3·62	7·39	4·45	2·12*	(0·09)	3·51	3·28	4·00
604	2·62	5·56	4·04	7·72	5·58	(1·60)	(0·26)	3·72	3·55	4·18
605	3·35	5·13	4·03	7·77	6·34	(0·77)	(0·29)	3·33	3·72	4·65
606	4·34	4·62	4·06	8·35	7·11	(0·28)	(0·12)	3·85	3·70	4·69
607	2·57*	4·99	5·63	8·73	5·94	(0·86)	(1·05)	4·09	3·92	4·19
608	(1·34)	4·35	5·07	7·41	5·08	(0·25)	(0·79)	2·82	4·12	3·92
609	(1·40)	4·69	(1·47)	7·39	5·11	(0·80)	2·27*	3·01	4·06	3·52

All highly significant except: *=significant at 5%.
( )=not significant.

TABLE 3. Percentage reflectance in offspring by age

Sons

	0–5 yrs (*n*=14)				5–12 yrs (*n*=83)				12–18 yrs (*n*=62)				18–35 yrs (*n*=14			
	Forehead		U.I.A.		Forehead		U.I.A.		Forehead		U.I.A.		Forehead		U.I.A.	
Filter	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
601	15·79	2·89	20·64	3·32	14·92	2·97	20·35	3·46	14·73	3·00	20·68	3·62	15·07	2·81	21·29	2·27
602	19·57	3·72	24·79	3·45	18·28	3·22	24·11	3·70	17·95	3·45	24·18	4·19	18·79	2·94	25·29	2·61
603	20·36	4·05	25·36	3·63	18·81	3·29	24·89	3·66	18·47	3·62	24·89	4·29	19·50	3·28	26·14	2·54
604	22·21	3·93	27·21	3·89	20·82	3·35	26·90	3·65	20·24	3·66	26·95	4·39	20·86	3·51	27·71	2·79
605	22·57	3·84	27·36	3·71	21·57	3·28	27·55	3·51	20·76	3·55	27·27	4·28	21·07	3·34	28·07	2·50
606	27·57	3·57	33·57	4·35	26·39	3·47	32·66	3·73	25·48	3·82	32·31	4·41	26·07	3·54	33·29	3·32
607	35·57	4·42	41·79	4·68	34·28	3·93	40·87	3·99	33·69	4·84	40·86	5·05	35·43	3·80	41·79	3·17
608	44·21	5·67	48·86	4·94	42·21	4·33	48·46	3·94	41·98	4·91	48·31	4·88	44·14	4·28	49·00	2·75
609	47·93	4·63	52·36	3·97	46·27	3·91	52·53	3·44	45·94	4·84	52·34	4·30	48·29	4·03	53·14	2·51

TABLE 3 (*continued*)

Daughters

	0–5 yrs ($n=7$)				5–12 yrs ($n=60$)				12–18 yrs ($n=78$)				18–35 yrs ($n=7$)			
	Forehead		U.I.A.		Forehead		U.I.A.		Forvhead		U.I.A.		Forehead		U.I.A.	
Filter	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
601	18·00	1·73	24·71	2·63	15·48	2·84	21·67	3·50	15·94	3·47	21·51	4·13	17·71	2·81	24·00	4·12
602	22·43	2·64	28·43	2·64	19·27	3·29	25·70	3·80	19·55	3·90	25·67	4·93	21·29	3·25	27·71	4·68
603	23·86	3·44	30·71	3·59	19·78	3·47	26·35	3·86	20·23	3·97	26·24	5·03	22·00	3·46	28·43	4·89
604	26·14	3·49	32·14	3·13	21·95	3·44	28·53	4·05	22·12	4·02	28·31	5·07	23·71	3·86	30·57	5·80
605	26·57	3·65	32·57	3·16	22·65	3·44	29·12	4·00	22·67	3·85	28·90	4·75	24·14	3·89	31·29	5·53
606	31·86	3·53	37·43	2·82	27·47	3·61	34·42	4·09	27·64	4·03	34·26	5·13	28·43	3·78	36·43	5·86
607	41·00	4·04	46·86	2·12	35·37	4·27	42·65	4·51	36·24	5·04	42·67	5·29	38·14	3·98	45·43	5·32
608	50·29	3·95	55·29	3·25	43·30	4·64	49·92	4·41	44·71	5·19	50·04	5·08	47·86	4·91	52·71	6·10
609	52·71	3·64	57·71	3·09	47·32	4·21	53·82	3·82	48·44	4·83	53·63	4·61	51·29	4·42	55·71	5·50

reflectance than the next two age groups, 5 to 18. This trend is relatively slight in the sons, clearer in the daughters. It is particularly distinct on the forehead and less pronounced at the upper inner arm. The two middle groups are generally similar to each other, though the standard deviations are consistently and clearly higher in the adolescent (13 to 18) than in the preadolescent (5 to 12) groups. The eldest age group again shows increased mean reflectance values at the upper inner arm over the two intermediate age groups in both sexes, and even above the youngest age group at most wavelengths in sons. In short these observations lend support to the hypothesis that some age effect exists, and that this is at least partly responsible for the lowered mean reflectance values of the offspring by comparison with their parents. Such an age effect may perhaps be due to the hormonal changes that occur during growth and especially those associated with adolescence. But it may perhaps be behavioural rather than biological, for the possibility of greater exposure of the skin in children is not ruled out.

Discussion

Interpretation of the results is complicated. There is the intrinsic difficulty of all biological characters such as skin pigmentation measured by spectrophotometry, where the mean reflectances and their variances are dependent on the optical characteristics of the filters used. Moreover there is the additional complication of scaling, for the measurements of reflectance are known not to be directly proportional to the underlying biological components of pigmentation, and the exact relationship between them remains to be worked out. The latter source of variation can be reduced, if not eliminated, by some suitable transformation, though in the present study this has not yet been done.

Comparison with Other Indian Samples

Has any change in pigmentation occurred in the Sikhs in England? Have they begun to differ from groups still in India? Unfortunately data on skin colour collected by spectrophotometry on Indian populations are piecemeal and incomplete, although Indian populations present a fascinating array of variations of skin pigmentation. Sikhs in India have not been examined for skin pigmentation, and the only other groups akin to them that have been studied are the

Khatris and Aroras of Punjab (Kalla 1969). These are the fairest at the red end of the spectrum of all groups studied in India, but this is not to say that they are the fairest Indian population, the Kashmiris in the extreme north of India, locked geographically in a beautiful mountain valley, are likely to be fairer still and to show more similarity to European populations in their pigmentation than any other Indian group. Moreover the Khatris and Aroras of Punjab have only been measured at 425 and 685 mμ so that a detailed comparison of them with the present Sikh sample cannot yet be attempted.

In contrast to the Sikhs, whose pigmentation falls at the upper limit of the range in Indian samples, are the low castes of Bengal (Buchi 1957, 1958) and Maharashtra (Das and Mukherjee 1963), while two tribal groups of Orissa, representative of the primitive indigenous groups of India have also been examined. Their comparison with the non-indigenous, later-coming Indian peoples emphasizes the magnitude of the diversity in pigmentation that occurs in the country.

Another caste group, of Baniya males and females, has also been studied (Kalla 1971). This is the third group in the caste hierarchy, and proves to be significantly darker than Sikhs although it shares the same environment as the Sikhs in the Punjab. In fact the Baniya seem to show closer similarity to the Bengali castes than to the Sikhs. This however does not imply any ethnic similarity between Baniya and the Bengali high castes, because the decreased reflectance of the Baniya is largely a manifestation of their endogenous genetic constitution, while the similarly dark skins of Bengali are more due to intermixture of several original strains of varying pigmentation, together with the vital environmental conditions favourable for skin tanning.

In London small samples of Bengali Brahmins, Kayasthas, Vaidyas and a heterogeneous group of north Indians studied by Tiwari (1963) all show relatively close resemblance to the Sikhs of the present study. There are moreover significant differences over all the visible spectrum between these Bengali caste groups and their contemporaries examined in India in two separate studies (Buchi 1957, 1958, Das and Mukherjee 1963). These findings may perhaps be partly ascribed to environmental similarity in Britain, to which both samples are exposed, though modification by environmental factors alone is unlikely to be the complete explanation.

So far then there is little information from peoples still in India sufficiently close to the present British Sikh sample to allow detailed comparison. The collection of such data from Sikhs remaining in India is essential to appreciate whether any pigmentation change is occurring in Sikhs in Britain, and preferably by examination of their relatives remaining in India.

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Summary

Study of skin colour in Sikh families in Britain shows as expected the reflectance profile to be more regular than in Europeans. Sex differences are more conspicuous in the offspring than in the adults, and the offspring tend to be generally darker on the upper inner arm than their parents. Age differences in pigmentation are suggested. There is insufficient evidence from India to discern whether any change in pigmentation has occurred in the Sikhs in England.

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BIOLOGICAL VARIABLES AND SOCIAL CLASS IN BIRMINGHAM

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SEVERAL surveys in recent years have examined the possibility that persons of different occupational groups may show differences in physical or psychological characteristics. The work of Schreider (1963) showed that French peasants differed from other workers in many characteristics, and Cliquet (1968) showed that certain physical variables were associated with upward social mobility.

In present society there is still a high level of assortative marriage for factors such as social class background, IQ and education (Garrison *et al.*, 1969). It might therefore be expected that this limitation of interbreeding would lead to variation in the frequencies of genetic marker traits between the social class groups. Such differences have been noted in the case of religious isolates in America and Japan (Glass 1952, Schull *et al.*, 1962) though the social class isolation here considered is less extreme. It has been suggested that the variation in IQ between social class groups represents differences in the genetic constitution of these classes (Burt 1959).

However in considering characteristics such as IQ and metric variables including height and weight, there is the added problem of environmental effects. Factors such as nutrition, family size, birth order and overcrowding have all been shown to affect the size of the individual. All of these factors are associated with social class, and it is difficult to separate the effects of any one factor.

In view of this problem it appeared logical to include, in a biological survey of different social class groups, some common genetic marker traits. These traits should be less liable to environmental influences, and so any frequency differences found would not be discounted owing to the "nature versus nurture" argument.

A previous study of the distribution of blood groups by social class from the Blood Transfusion Service data in Ireland had not given any evidence of social class differences for the ABO factors (Dawson 1964).

The present survey was initiated with the hope of comparing groups of workers from the extreme ends of the social class scale, using genetic and other biological marker traits as well as metric variables such as height for comparison. However it proved impossible to obtain an adult sample, and so it was decided to use schoolchildren as subjects.

As schoolchildren were used in the survey it was not possible to assign them to a social class rating of their own, but they were rated according to their father's occupation, using the Registrar General's Classification of occupations. It was also possible to compare children from selective and non-selective schools. Only children with all four grandparents born within the UK were included in the survey sample. The age range 14–15 years was chosen as being the oldest age group before the minimum school leaving age, though this range involved problems associated with the effects of puberty and the growth spurt.

A very wide range of traits was included in the survey: eye colour, hair colour, hair form, hair line (widow's peak), vision defects, colour vision defects, freckling of the skin, mid-digital hair, ear lobe attachment, cleft chin, relative finger length, ABO secretor status and PTC tasting. In addition the subject's height, weight, foot length and foot width were measured, and a laterality questionnaire of ten items was completed. The survey was carried out in the City schools by kind permission of the school staff.

Results

It was found that social class background was significantly associated with school type. This association had been expected in view of the available information on the distribution of IQ scores in the social class groups (Table 1).

There were in all five metric variables, as the height and weight variables were used to calculate ponderal indices. Of these it was found that the foot measurements showed no significant variation by social class. In height and weight it was possible to detect a trend to taller and heavier individuals at the more prestigious end of the

TABLE 1. Social class background by school type (percentage in brackets)

School type	Social class I	II	III	IV	V	Total
Selective	21 (6·7)	67 (21·4)	178 (56·9)	42 (13·4)	5 (1·6)	313
Non-selective	0 (0·0)	14 (5·5)	161 (63·4)	67 (26·4)	12 (4·7)	254
Total	21 (3·7)	81 (14·3)	339 (59·8)	109 (19·2)	17 (3·0)	567

social class scale. This was most marked in the male sample, where the social class I individuals had a mean advantage of 10·2 cm and 13·1 kg over the class V boys (Table 2).

TABLE 2. Mean metric variables by social class (Mean with S.E., sample size in brackets)

Sample		Height (cm)	Weight (kg)	Ponderal index
Male				
Social class I	(6)	170·3±3·8	61·0±5·5	43·7±0·7
II	(47)	164·7±1·3	56·1±2·0	43·4±0·3
III	(160)	168·4±3·8	53·3±0·8	44·9±0·9
IV	(44)	162·4±1·1	51·3±1·6	44·0±0·3
V	(8)	160·1±2·3	47·9±2·4	44·3±0·9
Professional	(53)	165·3±1·3	56·7±1·8	43·4±0·3
Manual	(64)	162·2±0·9	51·3±1·2	43·9±0·3
Female				
Social class I	(14)	158·6±1·8	53·6±1·6	42·1±0·6
II	(34)	159·7±1·0	53·3±1·3	42·6±0·4
III	(178)	158·0±0·5	51·9±0·6	42·5±0·1
IV	(64)	157·5±0·7	52·4±1·1	42·3±0·2
V	(9)	158·7±2·8	49·5±3·4	43·5±0·6
Professional	(48)	159·3±0·9	53·4±1·0	42·5±0·3
Manual	(91)	160·0±3·8	53·1±1·5	42·9±0·6

However, the number of individuals in the extreme social classes were small, and so for statistical purposes it was decided to combine social classes I and II to give a "professional" group, while classes IV and V were combined with those subjects of unknown social class to give a "manual" group. Even in this combined form it was found that the professional group of boys was 3·1 cm taller and 5·4 kg heavier than the manual boys. The ponderal index however showed no clear trend or significant differences between the social classes in males, this seeming to indicate that the differences lay in size rather than body build. In the height comparison, in males class I differed significantly from classes IV and V, while the professional group differed significantly from the manual group. There were significant weight differences between class I males and those of classes III and V, and the professional group differed from both class III and the manual group.

Among females there were no significant associations of metric traits with social class, and it was only in weight that any association similar to the boys' could be seen. The class I girls were 4·1 kg greater in mean weight than those of class V. The results for height and ponderal index showed little difference between the classes.

The association of metric variables with school type showed considerable differences between males and females. Among the females the selective school girls were taller and heavier, but in the male sample the non-selective group were taller, though the mean weights of the two male groups were similar. These differences were significant in the case of the female height comparison, and ponderal index comparisons between the two groups were also significant in both sexes (Table 3).

TABLE 3. Mean metric variables and school type (Mean with S.E., totals in brackets)

Sample		Height (cm)	Weight (kg)	Ponderal index
Male				
Selective	(146)	164·6±0·7	53·7±0·9	43·9±0·2
Non-selective	(131)	168·5±4·7	53·2±0·9	45·0±0·1
Female				
Selective	(177)	161·0±2·0	53·1±0·9	43·0±0·3
Non-selective	(140)	156·5±0·5	51·7±0·6	42·2±0·1

Only a minority of the marker traits were found to be associated with social class or school type. In the present survey it was impossible to diagnose vision defects, but the subjects were questioned as to their need to wear spectacles. It was found that the wearing of glasses differed significantly between the two school types, with more of the selective school children needing to wear glasses full time (Table 4)

TABLE 4. Vision defect by school type (percentages in brackets)

School type	Glasses full-time	Glasses part-time	Glasses not needed	Total
Selective	43 (13·3)	37 (11·4)	244 (75·3)	324
Non-selective	19 (7·8)	29 (10·7)	224 (82·4)	272
Total	62 (10·4)	66 (11·1)	468 (78·5)	596

The ability to taste phenylthiocarbamide is a well known polymorphism, and in this survey the subjects' taste thresholds were determined by use of the Harris and Kalmus (1949) method. This gives results which may be examined in two forms—either as a two

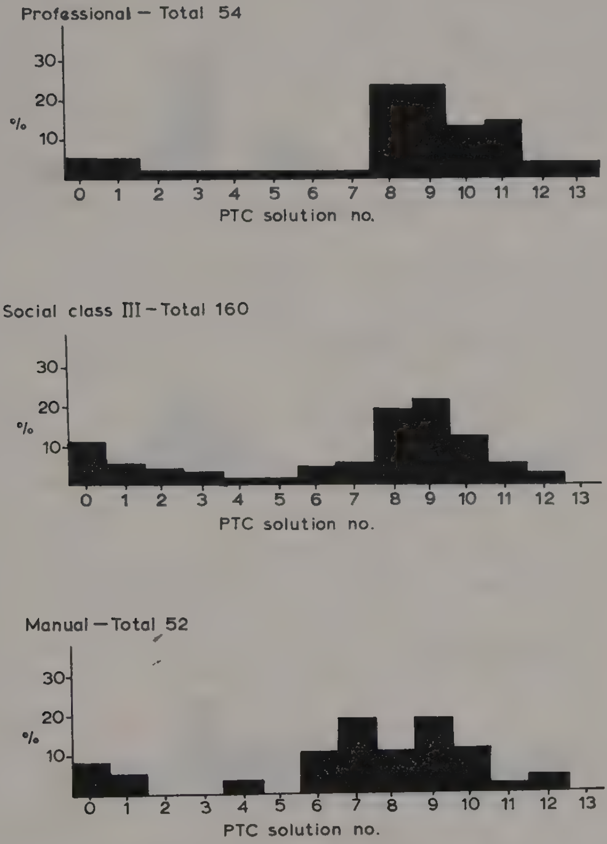

Fig. 1a. PTC taste threshold distribution by class group in male sample

class "taster"/"non-taster" variable, or as a complete frequency distribution. It was found that there was no significant association of social class with PTC tasting when the two class form of data was used. However when the whole distributions were compared it was found that there were significant differences between the professional and manual groups in males, and in the females the manual group differed significantly from class III and from the class III and professional groups combined. (Figs. 1a, 1b). The Kolmogorov–Smirnov test was used in comparisons of the whole taste threshold distributions.

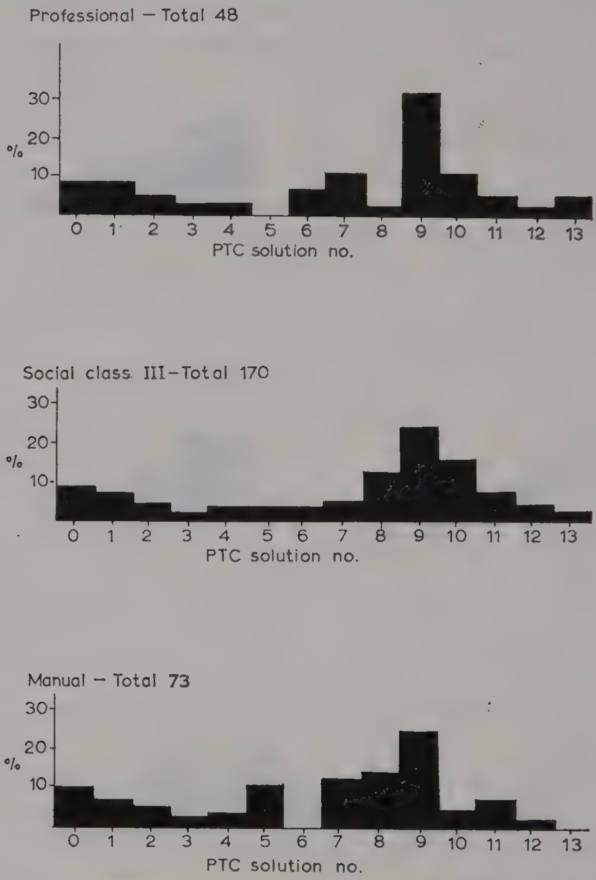

Fig. 1b. PTC taste threshold distribution by class group in female sample

The remaining significant associations were between cleft chin and both social class and school type, and between hair line (possession of a widow's peak) and school type. In both these characteristic the assessment of the trait was carried out by reference to a standard picture scale, but it is felt that the assessment was free from bias. In the association of cleft chin with school type the same trend could be seen in both sex samples, but this was only significant in the female group (Table 5). In contrast the association of cleft chin and social class group was significant amongst the males but not the females (Tables 6). The results for the comparisons of hair line types showed that both single sex samples had a significantly higher frequency of persons with widow's peaks in the grammar school group (Table 7).

TABLE 5. Cleft chin by school type (percentage in brackets)

School type	Male		Female	
	Cleft	Non-cleft	Cleft	Non-cleft
Selective	44 (29·7)	104 (70·3)	40 (22·6)	137 (77·4)
Non-selective	54 (41·2)	77 (58·8)	49 (34·8)	92 (65·2)
Total	98 (35·1)	181 (64·9)	89 (28·0)	229 (72·0)

TABLE 6. Cleft chin by social class (percentages in brackets)

Class group	Male		Female	
	Cleft	Non-cleft	Cleft	Non-cleft
Professional	11 (20·4)	43 (79·6)	9 (18·7)	39 (81·3)
Middle	54 (33·7)	106 (66·3)	49 (27·4)	130 (72·6)
Manual	29 (54·7)	24 (45·3)	24 (32·9)	49 (67·1)
Total	94 (35·2)	173 (64·8)	82 (27·3)	218 (72·7)

TABLE 7. Hair line (widow's peak) by school type (percentages in brackets)

School type	Male		Female	
	Widows peak	No peak	Widows peak	No peak
Selective	41 (27·9)	106 (72·1)	31 (17·6)	145 (82·4)
Non-selective	19 (14·5)	112 (85·4)	12 (8·5)	129 (91·5)
Total	60 (21·6)	218 (78·4)	43 (13·6)	274 (86·4)

In the laterality comparisons it was found that left-handedness in two activities was significantly associated with school type, though this association was present only among the boys. For these activities, writing and dealing cards, it was noted that the non-selective boys showed excesses of 10·2 per cent and 11·8 per cent left-handed persons. However in the female sample there was a tendency for the selective school girls to have the higher frequency of left-handed persons (Tables 8 and 9).

TABLE 8. Writing by school type (percentages in brackets)

School type	Male		Female	
	Left	Right	Left	Rhigt
Selective	12 (8·1)	136 (91·9)	16 (9·1)	160 (90·9)
Non-selective	24 (18·3)	107 (81·7)	13 (9·2)	128 (90·8)
Total	36 (12·9)	243 (87·1)	27 (9·1)	288 (90·9)

TABLE 9. Dealing cards by school type (percentages in brackets)

School type	Male		Female	
	Left	Right	Left	Right
Selective	27 (18·4)	120 (81·6)	29 (16·5)	146 (83·4)
Non-selective	39 (30·2)	90 (69·8)	17 (12·2)	122 (87·8)
Total	66 (23·9)	210 (76·1)	46 (14·6)	268 (85·4)

The results of this survey have shown that it is possible to demonstrate differences in the frequencies of marker traits among social class groups, despite the use of far from ideal survey subjects. The present survey results for the association of metric variables and social class are in good agreement with those of many previous workers (Tanner 1966, Topps *et al.*, 1970). Indeed it might have been expected that a more definite association would be demonstrated. The opposing trends of size in association with school type are difficult to explain, but it may be that the age of the sample has complicated the problem. All the previous reports on sizes of children at different types of school have indicated that children of greater ability tend to be larger than their less able fellows (Tanner 1966).

In conclusion it is felt that, if social class differences can be found in a sample of children from a socially mobile area such as Birmingham, then the possibility of finding differences between groups of adults in stable occupations is even greater. A full survey comparison of adult occupational classes is needed, though obtaining suitable and willing survey subjects will constitute a major problem.

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DERMATOGLYPHIC DETECTION OF LOCAL GENETIC VARIATION

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EXACTLY 80 years ago, Francis Galton suggested that variation in dermal traits existed on a very local scale in Britain. He wrote, in *Finger Prints* (1892), "Local dermatoglyphic peculiarities exist in England, the children in some schools in some localities seeming to be statistically more alike in their patterns than English children generally". In Germany, in the 1930's, Abel and then Poll, showed considerable variation in finger and palmar pattern frequencies among various regional subsamples, and, more recently, Newman has written of dermatoglyphic variation between Highland and Lowland Mayan groups in Yucatan. Nevertheless, despite the suggested high heritability of certain dermal features (total ridge count for instance has a heritability estimated by Holt (1957) at 95 per cent), remarkably little attention has been given to the use of dermatoglyphics in the investigation of local and regional differences among populations.

At the Guildford meeting of this Society last year, I reported on a study carried out in Oxfordshire and Berkshire during 1962 to 1966 showing that differences do exist within this region, and on a much more local scale than hitherto envisaged, using the ridge counts and patterns of the fingers as an investigatory tool. Today I will review these findings briefly and discuss some attempts at more sophisticated methods of analysis.

The area of the south Midlands covered by this survey consists of those parts of the county of Oxfordshire lying west of the Cherwell in the north and to the south of the Oxfordshire clay vale, together with West Berkshire north of the Kennet. The area is bounded by the Cotswolds in the north, and divided by the river Thames and by the ranges of the Downs and Chilterns in the south. Predominantly rural until very recently, the growth of industrial centres such as Banbury, Didcot, Reading, and especially of Oxford itself, is now attracting population from far outside the region.

The sample consisted of the prints of 1193 male and 1365 female schoolchildren, from secondary day schools. Every child had one or both parents born locally, within a radius of 15 miles of the child's home. Sibs were, of course, excluded from the data.

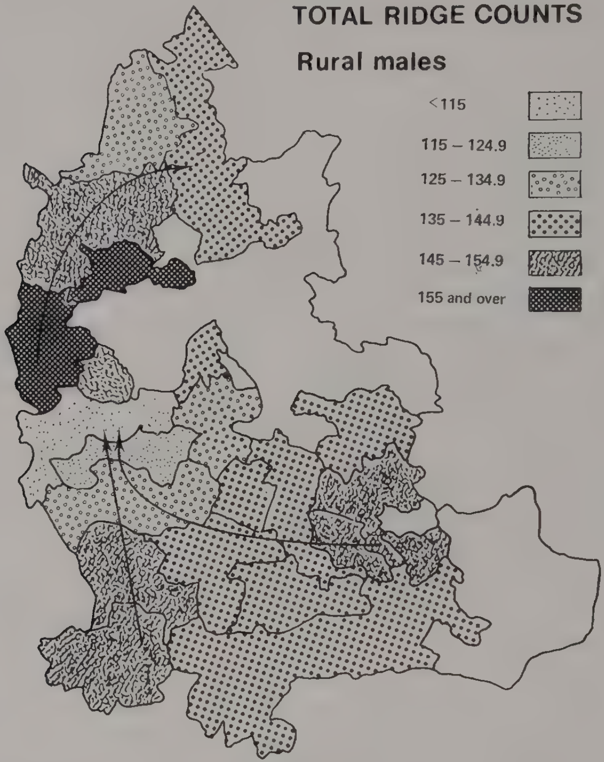

FIG. 1a

The material for analysis consisted of the ridge counts and pattern types of the finger tips. Finger ridge count is measured as the number of ridges crossing or touching a line drawn between the triradius of each pattern and its centre. The ten finger counts were summed to give the total ridge count (TRC) for that individual. The patterns of the finger tips were subdivided very simply into whorl, loop, and arch according to the methods described in Henry (1901), and Cummins and Midlo (1943). Finger ridge count and pattern type are established very early in foetal life, and do not change afterwards, except as a result of serious injury to the epidermis.

The resulting data were subdivided first, into male and female, and then into rural and urban samples, towns of 5000 and more inhabitants being regarded as urban centres. The rural data were further subdivided, within the county divisions, into subsamples consisting of blocks of like parishes, on the basis of topography, human ecology and local history. This further rural subdivision resulted in 12 locality samples in Berkshire, 6 in north Oxfordshire, and 4 in south Oxfordshire.

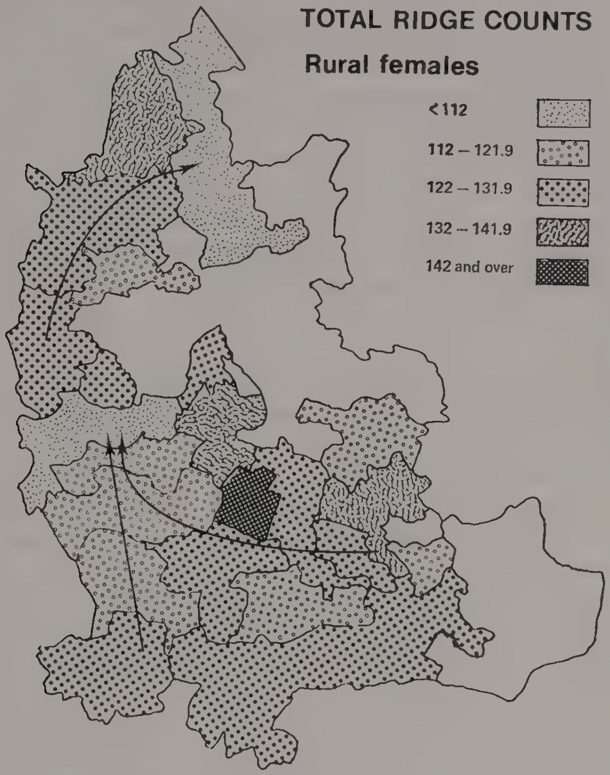

FIG. 1b

A strong clinal pattern is evident from inspection of sample mean TRC, despite the necessarily small size of many of the samples

(Fig. 1). Full data are given elsewhere (Roberts and Coope 1972). The high means of the Cotswolds in north Oxfordshire decline eastwards and northwards to Banbury and the Cherwell valley. Southwards, the means drop sharply to the focus of very low values around Faringdon and Wantage, and then gradually rise over the Berkshire Downs and northeast Berkshire, to the high means of the Thames and Kennet valleys. This area of high mean TRC is extended further eastwards into south Oxfordshire but with slightly lower means along the edge of the Oxfordshire plain in the north than elsewhere in this region.

These clines in mean TRC are striking in the rural males. They are less evident in the female samples, on account of local elevation in Didcot (sample of 12 only) and Hook Norton but are still distinguishable. They are clearer in the rural than the urban data, perhaps as a result of the greater immigration into the towns of people from outside the region and from other parts of the region itself, with consequent blurring of the clinal nature of variation in dermal features.

Statistically, highly significant differences emerged among the constituent rural samples, suggesting that the population of the area is highly heterogeneous for this trait. In male and female alike, significant differences were found overall; among the 6 local subdivisions of the north Oxfordshire sample; and among the 12 localities of Berkshire, mainly due to the clinal distribution across northwest, central, and south Berkshire. No significant differences were found among the localities of south Oxfordshire.

Limited qualitative analysis of the finger patterns gave similar findings, indicating the existence of local, and of regional variation in this area of the south Midlands. Areas of low TRC tended to have fewer whorls and more loop and arch patterns than did areas of high TRC, with more whorls and fewer arches. There is known to be a high correlation between finger ridge count and triradius number (Pons, 1962, Parsons, 1964).

Since almost all variation in TRC is genetic, this study shows that considerable genetic heterogeneity still existed until recently within the Oxford region, despite the growing accessibility and population movement in the area. That this heterogeneity is clinal in nature, gradients extending northeast from the high ridge counts of the Oxfordshire Cotswolds, and south and east from the low ridge counts of the area around Wantage and Faringdon in northwest

Berkshire, and that there is extensive parallelism between male and female samples, and, to a lesser extent, between urban and rural data, reinforce the strong impression of real genetic variation in this area.

The biological significance of these differences, in finger ridge count and pattern type, is difficult to explain convincingly with our present relative lack of knowledge of other genetic variation in this region, and of the action of natural selection and other genetic forces, and even of gene action itself, on these traits. Should these population differences be explained in terms of the original settlement and subsequent local history of this region, or in terms of the action of genetic processes such as selection and possibly drift on the gene frequencies of certain sections of the population, or by a combination of these factors?

As a possible historical explanation of these differences, we know, for instance, from archaeological evidence, that the distinctive low ridge count area in northwest Berkshire was first settled by Neolithic peoples coming northwards over the Downs from the south. Fleure and Whitehouse (1916) remarked that the villages along the Wantage Heights showed evidence of the valleyward movement of Neolithic peoples, as the water table of such chalk uplands fell. There appears to have been Saxon penetration via the Wash rivers. Later, this area was isolated from the main routeways east and west, north and south across the region, and the limited mobility in this wholly rural community may have helped to preserve what distinctive dermal features the population of the area originally had. Similar considerations may apply to the high TRC area of North Oxfordshire, a major settlement area of the Anglo-Saxon Hwicce coming in from their main tribal lands in neighbouring Gloucestershire, Worcestershire and Warwickshire to the west. The Hwicce gave their name to the Cotswold forest of Wychwood, whose inhabitants impressed Buxton, Trevor and Blackwood (1939) by their comparative darkness relative to the surrounding population.

If such original differences existed, have they been maintained by geographical isolation, and indeed possibly intensified further by localized natural selection? Are multigenic traits, as Newman (1960) suggested, more resistant to chance and sudden effects on gene frequencies than single gene traits, and do they possibly reflect population relationships older and more stable over time?

Only further studies, with larger dermatoglyphic samples, and with parallel studies of other traits known to have a strong genetic component, can prove or disprove such theories, and it is unlikely that, until these are available, the reasons for these remarkable differences between populations in the Oxford region can be stated authoritatively.

Discriminant Analysis

During the analysis of these dermatoglyphic data, it became obvious that the traditional statistical treatment of such multigenic traits was subject to many inadequacies and shortcomings. The second part of this paper, therefore, discusses exploratory work on the use of multivariate statistics in the examination of such differences between populations.

Analysis of variance of mean TRC is a crude and inefficient way of evaluating population differences, crude, because mean TRC is merely the sum of the ten finger counts and does not take into account their individual characteristics, and inefficient because mean TRC gives no measure of biological distance, except in gross terms of statistical significance. Of the traditional methods of averaging pattern type frequencies, Francis Galton wrote (1892), "This coarse statistical treatment leaves an inadequate impression, each digit and each hand having its own peculiarity. . . . The statistics of the digits must be separated, and not massed indiscriminately" (page 115). Bonnevie (1924) and later Holt (1957) confirmed the statistical individuality of each finger indicating, for instance, that the fingers nearer each other are more alike in ridge count and pattern type than the fingers further apart on the hand. To sum the ten fingers, then, in one statistic glosses over differences that are statistically, and also biologically, significant. Very different populations have very similar TRC means. A sample of Aberdeenshire Scots, for instance, with a mean TRC of 133 is very like the Ecuadorian Jivaro (Sunderland and Coope 1969) with a mean of 137, and yet the size of loops on the thumb, as measured by finger ridge count, is very different in the two populations.

Multivariate analysis, alternatively, is concerned with the analysis of multiple and related measurements, like the ridge counts of the ten fingers, made on samples of individuals, and treats these measurements mathematically as the discrete yet interdependent parts of the whole, in this case the hand. The individual peculiarities of each finger are not submerged in this type of analysis, but are the principal factors distinguishing between the populations.

The two multivariate statistics used here as measurements of population distance, are the Mahalanobis D^2 and the probability of misclassification. Mahalanobis' D^2 provides a measure of generalized distance by which to plot differences between the samples on a single unitary scale using all the finger ridge counts simultaneously, through the agency of a single linear function derived from them. Trevor, who applied the techniques of discriminant analysis to his anthropometric data on the Sandawe (1947), commented that Mahalanobis' D^2 was "The most promising analytical instrument yet designed for the measurement of the 'distances' between populations where adequate data are available". The probability of misclassification is a statistic giving the probability of classifying an individual as belonging to either of the populations instead of absolutely assigned to one of them, when discriminant analysis is applied to the data.

In applying these measures, each individual was characterized by a vector of 20 ridge counts (one radial, one ulnar on each of ten fingers), for our work on factors influencing ridge count shows important contributions to be made by all. The long and complex computation of these statistics was done on the SRC Atlas computer at Chilton, using the Ascop statistical package. The mathematical assumptions inherent in multivariate analysis were considered to be satisfied, after examination of the variances and covariances of the population matrices.

The basic test of the discriminant function, in the context of population dermatoglyphic work, was considered to be its ability to discriminate successfully between male and female samples. One of the types of population variation that exists in every population so far studied is the between-sex variation in dermal traits. Female samples almost invariably have lower mean finger ridge counts than male samples, and corresponding differences in overall proportions of pattern type, with fewer whorls and more arches and loops. These fundamental differences should be capable of detection and quantification by the discriminant function; if they are not detected, then this analysis should not be applied to more debatable data.

Relatively little is known about the genetic background of the differences between males and females in finger ridge count and pattern type, but they are thought by Penrose (1967) to be the result of sex-influence, the X chromosome having a far greater effect on this trait than the Y chromosome, although the trait itself is considered to be autosomal. Penrose further suggested that this influence is non-specific and acts by affecting the size and chemical constitution of the foetal finger pads, the differential pressures of tension and compression creating different types of ridged area.

The Berkshire data of 675 males and 800 females were therefore subjected to discriminant analysis. The resulting D^2 statistic of 0·31 was significant at the 1 per cent level, and the probability of not being able distinctly to classify an individual as either male or female was very low indeed, possibly due to the large range of phenotypic variation in this sample of nearly 1500 individuals. This is obviously a very powerful statistic when used on samples of comparable size.

Encouraged by the sensitiveness of the discriminant function when applied to between-sex differences, I then examined within-sex differences between populations, taking four populations geographically, historically, and culturally distinct; a sample of Aberdeenshire Scots, Basques from the Spanish Pyrenees, Samaritans living at Nablus (Jordan), and the Ecuadorian Jivaro.

The D^2 values increased as biological distance grew. In the female samples, the smallest D^2 distance of 0·78 occurred between Scots and Basques, a distance of 2·47 between Scots and Samaritans, and the largest 4·44, between Scots and Jivaro (Table 1). The two male distances computed tended to be smaller than but parallel to the female ones. These distances are all much greater than the between-sex distance computed on the Berkshire data (0·31). D^2 distances appear to bear no direct relationship to differences in sample mean TRC. Scots and Jivaro males have very similar mean

TABLE 1.

Sample means and D^2 distances

	♂		♀	
	n.	mean TRC	n.	mean TRC
Scots	58	132·86	88	127·85
Basques	—	—	76	127·59
Samaritans	60	152·40	49	146·08
Jivaro	129	136·80	110	135·89
		D^2		D^2
Scots/Basques		—		0·78
Scots/Samaritans		1·77		2·47
Scots/Jivaro		2·38		4·44

TRC's of 133 and 137 ridges respectively, but a larger D^2 statistic than that of the Scots and Samaritans, with mean TRC's of 133 and 152 ridges respectively. The female Scots were similarly more like the Jivaro than the Samaritans in mean TRC. This lack of agreement between D^2 distance and sample mean TRC is not unexpected, since the discriminant analysis deals with the characteristics and interrelationships of the finger ridge counts, and analysis of TRC with the gross individual summation of these values.

With the increase in distance, as expressed by the D^2 statistic, the probability of wrongly misclassifying individuals between these populations decreased sharply, but, possibly partly because the relatively small samples were not fully representative of the range of phenotypes to be found in each population, these probabilities, except for that between Scots and Jivaro females were not so small as in the Berkshire data. It is interesting that the female samples, which have also been shown to be the more variable, provide better discrimination between these populations, than do the male samples.

These discriminant analyses were performed on necessarily small samples, the smallest being the 49 Samaritan females, and the largest the 129 Jivaro males—only a seventh the size of one of the Berkshire samples. Yet, despite these small sample sizes, with the resulting distortion of phenotype frequencies, the D^2 results are consistent both between sexes, and with biological, cultural and geographical reality.

The discriminant function has thus, I feel, adequately demonstrated its capability to provide a meaningful distance statistic with which to measure differences between populations using finger ridge count data. It now remains to apply discriminant analyses to the south Midlands data in order to distinguish within and between group relationships among the various locality subsamples described above. How closely will the results of this analysis parallel the clines in mean TRC described in the first half of this paper? What will be the status of the samples, intermediate in mean TRC between the high and low ridge count areas, and also of the urban data? Will the between-sex differences vary consistently and meaningfully between the various subsamples? How will the amount of variation found in the Oxford region compare with that to be found elsewhere, in terms of the D^2 statistic? How will the D^2 distances computed on dermatoglyphic data compare with those computed on other multivariate measurements from the same population series? All these questions, and more, wait for the discriminant analyses to answer.

The use of the discriminant function in the statistical treatment of such multivariate data, now computationally feasible because of the development of large and complex computers, must from the evidence adduced above, help in clarifying and evaluating the large amount of genetic variation that is still to be found between local and regional populations in Britain.

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